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THE GLACIAL BORDER — CLIMATIC, SOIL, AND BIOTIC FEATURES

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VEGETATION AND CRYOPLANATION

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The general subject of this symposium is the behavior of plants, animals, and biotic communities with relation to the southern boundary of the glacial tills and other deposits that date from the Pleistocene ice advances. There is in this subject the assumption, or at least the working hypothesis, that the glacial boundary *has* significance to the present distribution and behavior of the living inhabitants.

There is no question that the boundary is a demonstrable fact, and that it is marked by differences in soils and land forms. Furthermore, it has a historical significance. There is in our subject the further hypothesis that the behavior of the biota and biotic communities on either side of the boundary is related in some way to historical facts rather than to present ones alone. There is a suggestion that the occurrence and local distribution of the biota cannot be understood simply by analysis of climatic, edaphic, and biotic factors of the environment on either side of the boundary at a point in time, but that they must be interpreted also in the light of the history and inheritance of the organisms themselves in relation to the history of the soils and land surfaces. In brief, it is suggested that to reach a reasonable understanding of the present behavior of the biota we should endeavor to reconstruct the landscapes in the region of the glacial boundary as they have developed in postglacial time.

In whatever way we choose to interpret the biota and its geography, we must begin with "site" or "fundament." There must be a "place" into which the biological elements of the landscape can come. American plant geographers, with their predilection for the "dynamics" of vegetation, have always been greatly concerned with land surfaces and soils. They have been particularly concerned with the mutability of the terrain because of their emphasis upon the study of vegetational change. We have experimented with interpretations of climatic change in a few places, particularly in the West, but we have built our ideas of vegetational development very largely upon physiographic change.

Out of this has come what we commonly call "physiographic ecology." Although some of its roots are to be found in a few isolated ideas derived from the Old World, physiographic ecology is based principally upon an American idea, developed in the temperate parts of the upper Mississippi basin and the Great Lakes region. It had its beginnings about 50 years ago when the terms "peneplain," "monadnock," and "cycle of erosion" became current in physiographic study. This was the period in which modern physiography was growing in America under the influence of W. M. Davis (1909) and his co-workers. There appeared the idea of a cycle of erosion wherein mature topography, uplifted by diastrophism, was rendered youthful again through renewed erosion, by running water, of the old surfaces. Upland water tables would then be lowered, and materials derived from the uplands would be transported and deposited again on flood plains, upon which would be re-established a degree of physical stability. There were, of course, many variations of this theme of the mutability of the terrain, but the principal agents of change were usually running water or wind.

In such an ideological setting there was fertile ground for the development of ideas of change in the botanical landscape. We had a series of research projects whose results have become classic in American plant ecology. Cowles (1901) produced his masterly analysis of the vegetation of the Chicago region, and cleverly related vegetational development to the evolution of land forms. He made an equally searching study of the great sand dune areas at the south end of Lake Michigan (Cowles, 1899). Transeau (1903, 1905-06) took up the study of the development of vegetation on poorly drained land, and presented papers on the bog plant societies of North America. Jennings (1909) caught the idea of relating vegetational development to certain shore forms on the Great Lakes. All of these papers appeared within a period of ten years, between 1899 and 1909. The ideas were carried further, with considerable broadening, by Miss Braun (1916) in her physiographic ecology of the Cincinnati region, and by Nichols (1913-20) with his vegetation of Connecticut.

In more recent years the idea has been given still wider application by Fernald (1931) in his detailed studies of species distribution and specific differentiation in eastern North America, and by Miss Braun (1940) with her description and analysis of the undifferentiated deciduous forest communities of the ancient Appalachian Plateaux. Here the idea has been carried beyond local application restricted to relatively small areas, and has been applied on a geologic time scale, involving changes of land surfaces and vegetations dating into the Tertiary. Clements (1916) went still further and conceived of gigantic succession complexes that might be related to the great geologic eras of the earth.

This idea, with all its ramifications, has become a part of the very fabric of our thinking in plant geography. Almost without our knowing it, the idea has greatly influenced some of our most basic concepts, such as that of the plant association and the nature of succession.

The idea was worked out in the temperate parts of North America, a fact which is commonly lost sight of in our preoccupation with the complex problems to which it has given rise. One of the primary characteristics of the development of land forms in this region is the existence of periods of relative physical stability in the soils. Considerable periods of time are required to erode an uplifted surface and to deposit its materials elsewhere. During these processes there are times of stability which are long enough to embrace many generations of our longest lived plants. This applies in varying degrees to the time it takes to fill a pond with vegetation, or to reactivate a sand dune, or to move a sand spit along the shore of a lake.

In these times of physical stability in the soils, complex communities of plants and animals have time to form, and what we call "dominance" almost invariably appears in them. The vegetation has time to react upon the raw fundament, and plant communities by their life and development alter the sites upon which they

occur. The phenomenon of succession appears, and many students have gone so far as to use a "biological" definition of succession, wherein it is conceived that the only true succession is one that is brought about by the reaction of plants and plant communities upon the site and upon each other (Phillips, 1935).

Some of us have tried to work out plant successions outside of the temperate zone. To put the matter mildly, we have had difficulties in applying the ideas derived from our training and experience in the temperate regions. We have found that the farther we go, phytogeographically, toward the Arctic or the Tropics the greater the difficulties become. It is only natural that we should carry our methodologies and assumptions with us as we go, and it is also natural that we should be loath to discard or seriously modify them when we find them inadequate.

One of the first questions that arises is in the application of the idea of dominance to complex communities. In the arctic and alpine tundra we have communities of relatively few species, but when one tries to describe them in terms of dominance or primary species he finds himself merely listing a considerable part of the flora. Antevs (1932) had this difficulty when he was describing the alpine communities in the White Mountains of New England, and Polunin (1934-35) found it extremely difficult to do at Akpatok Island. Polunin's (1948) recent study of plant communities in the Eastern Arctic resolves itself into a compendium of variable species complexes that reappear with endless variety in one locality after another. It was this that Griggs (1934) was talking about when he said that the tundra flora of Alaska acted like a ruderal or weedy flora with no apparent rhyme or reason in its local assemblages. In all of these cases, we see a prime characteristic of temperate vegetation non-existent or very poorly developed in the Arctic.

Another of the attributes of plant communities, successional development, also becomes extremely difficult to document and prove as we go away from the temperate zone. Vegetational change does occur naturally, but to establish it within a "biological" definition, or in terms of any physiographic progression with which we are familiar, commonly becomes impossible.

In the boreal regions of America, we deal with topography which in many cases is extremely youthful. Water tables and lake shores fluctuate much more than they do in the temperate zone. One wonders what would happen to our ideas of the development of vegetation on the shores of Lake Erie if the water level of this lake should rise 8 or 10 feet every 50 years or so and then return to its former level; but that is what happens at Lake Athabaska. Whole lake basins composed of myriads of small bodies of water interspersed with swamps and bogs are having their ground water levels reduced by the erosion of friable barriers such as glacial moraines. Other lakes are being formed as "thaw lakes" in areas underlain by perennially frozen ground (Hopkins, 1949). Such bodies of water appear, develop marginal vegetation and then disappear when the vagaries of seasonal thaws open underground drainage channels. Ice-push is enormously effective in modifying shore forms, and is a factor which is insignificant in most of the temperate zone. The result is that vegetation around lakes and ponds in the far north commonly gives but little indication of regular successional stages in the development of organic deposits.

Perhaps the most nearly authentic natural successions in the North, with the exception of a few secondary ones, are on river islands and flood plains. Here again, however, excessive flooding due to damming by ice and driftwood is so common that it becomes difficult to infer natural biological successions.

Evidences of succession in the Arctic, when they are carefully examined, commonly prove to be so fragmentary and so isolated in the total context of the vegetation that they cannot be strung together into recognizable trends toward equilibrium. Approaches to equilibrium or relative stability, such as we find in temperate regions and are wont to call "climaxes," are almost impossible to define

in the Arctic and much of the Subarctic. At best they are ephemeral in time and space.

With the ideas of dominance and succession so difficult to apply in the North, it behooves us to re-examine some of our basic premises with regard to the relations between the development of vegetation and the development of land forms. Dominance and succession are both basic attributes of vegetation in the temperate regions, and I have suggested above that they both arise from a degree of physical stability which in turn is a fundamental attribute of the land surfaces. We are entitled to ask whether there can be something wrong with the physiographic premises upon which we are basing our work in the boreal regions.

The student of land forms brought up in temperate America, when he goes into the boreal regions, sees a great variety of forms with which he is totally unfamiliar. He is apt to be as bewildered as a northern botanist who makes his



FIGURE 1. Stone polygons on a limestone mountain in northeastern British Columbia. The fine-textured materials in the centers of the polygons are so actively "churned" by frost action that only a few hardy plants can withstand the frequent physical disturbance of the soil.

first excursion into the tropics. Our physiographer has learned that it is possible for rocks to be cracked by frost. But he has never seen such active frost riving as he sees in the Arctic and Subarctic. Large boulders are commonly broken into little pieces by frost, with all the fragments lying about in the vicinity. He will see massive angular boulders lying about a central core. With heavy machinery he could put them back together to form a rock as big as a house, and he is forced to the conclusion that the frost riving he sees now is child's play to what must have occurred in the past.

He comes upon great fields of rock, called "block fields," that are composed of large boulders, many of them angular, and obviously formed by the break-up of still larger ones. No physiographic process that he has ever heard of in the temperate zone is adequate to explain them.

The land surface is marked by a multitude of terrace forms. Some of these are several feet high and many feet long. Others are tiny affairs, only a few

inches high and wide. If he has the time to dig trenches through such terraces, he finds that many of them are still active in formation and movement.

On more or less level surfaces he is confronted with curious polygonal arrangements of materials. The polygons may be composed of fine or coarse material,



FIGURE 2. Large "fossil" stone rings in southwestern Yukon, 6-10 feet in diameter.



FIGURE 3. Cryoplanation terraces on a tundra-covered mountain slope in southwestern Yukon.

and they may vary in size from the width of his hand to many feet. On slopes he finds long stripes of loose stone trending at right angles to the contours, and on very gentle slopes he finds these stripes merging into a series of combinations with the polygonal arrangement. A surprising proportion of the stones will be found to be standing on edge. On high mountain slopes, he will see remnants of bed

rock standing up above the general level like monuments. These remnants are exfoliating actively, breaking up under the influence of frost. They have a configuration in profile which is utterly strange to him, because, although they are rapidly disintegrating, there is no talus accumulation at their bases. In fact, they are apt to show some overhang at the base. The surfaces of the gentle slopes below these monuments are strewn with rock fragments that have fallen from them, and it is obvious that the fragments are moving away down slope from the base faster than they can accumulate.

He will be impressed by the relative insignificance of stream cutting and deposit. Flood plains are small in breadth and depth. There is very little evidence of these processes except where great glacial streams issue from the mountains. Another striking feature of the landscape is the broad rounding of slopes. The general contours of these slopes are not those that we have learned to associate with down cutting by streams.

From all of these observations, our student of land forms gets the impression that the surface materials of the land are in motion, slow motion though it may be. He must also conclude that this motion has been more active at some time in the past than it is now. He soon begins to associate most of these features with the action of frost upon the soils.

Each year in the boreal regions the ground freezes to great depths. In many parts of the Arctic and Subarctic there is perennially frozen ground beneath the surface. In fact, it is now computed that about one-fifth of the earth's surface is underlain by perennially frozen ground (Jenness, 1949). During the spring of each year the surface materials thaw out. But there is a relatively long period during which the temperature fluctuates diurnally around the freezing point. Each time the water in the soil freezes it expands; and the effective expansion is in a direction at right angles to the freezing surface. When the soil thaws again its particles fall vertically, so that if the surface has any slope, they tend to move down grade. It is obvious that if freezing and thawing are to be effective, there must be a supply of water. One of the characteristics of freezing soil is that it can absorb and hold much more water than unfrozen soil. It has a tendency to absorb water as it freezes (Taber, 1943). Consequently many frozen soils are water-logged so that when they thaw they are almost fluid and have a tendency to flow down slope en masse. This greatly enhances the rate of movement of materials.

From the standpoint of vegetation, one of the principal results of this process is instability. The soils, even under forest or heavy turf, will move, often in masses. The result is the physical dislodgment of growing plants. This process is so widespread in arctic and subarctic lands that its effect upon vegetation is of primary significance. In thinking about the development of plant communities on such surfaces, we must become accustomed to thinking in terms of a relatively permanent physical instability of the soils.

It appears clear that the very bases upon which our concepts of dominance and primary biological succession have developed—the relative stability of surfaces—do not exist over wide areas in the boreal regions. It follows that vegetational dynamics in general for these regions must be developed upon a new conception of land form dynamics.

The study of arctic and subarctic land forms is still in its infancy though rapid progress is now being made. The United States Geological Survey, through its Alaska Terrain and Permafrost Section, has been concentrating on the problem during the past three or four years, and we are beginning to find some order in the chaos of newly observed facts. New aspects of the problem, however, are appearing constantly, and undescribed land forms due to frost are turning up each time a party goes into the field. There is beginning to appear, however, a concept of the molding of the landscape by frost action. It is called "cryoplanation," as opposed, perhaps, to peneplanation in temperate regions (Bryan, 1946).

Soils that owe their form and texture to frost action are now being called "congeliturbates," and the process that forms them is called "congeliturbation."

Some curious reversals of our commonly accepted ideas have developed. On a steep mountain slope, for instance, we are accustomed to thinking of small rocky stream channels and gullies as the most unstable plant habitats. In the Arctic, on the other hand, such stream channels, though they are very poorly represented, turn out to be the most stable habitats, for the presence of even a small running stream has a tendency to lower the water table slightly and so cut the supply of water to the surface soils immediately along its banks. The principal effect of this is to lessen the activity of frost, so that the materials along the banks of the stream actually stay in place for longer times than those on surfaces without streams.

Forests that develop on actively moving slopes are more or less unstable depending upon the degree of slope and drainage of the soils. The mortality in such



FIGURE 4. "Drunken forest" of black spruce growing on frost-heaved soil, in southwestern Yukon. Scarcely a tree is straight and vertical, and mortality is high.

forests is high, because when masses of soil move they have a tendency to tear the root systems of the trees loose from their intimate soil contacts. If the break is not too serious the trees can recover, but many of them do not. It is not uncommon to find 25% of the standing trees in a forest dead. Examination of growth rings shows that the trees have been subjected to this influence repeatedly. The evidence is in sudden suppressions of growth, with subsequent gradual adjustment. Usually no two trees show the same series of suppressions, even though they may be within ten feet of each other, because the soils move in finite masses which may be only a few feet in diameter. A characteristic of these forests is the large number of leaning trees which have been tipped over by the movement of the soils.

In the region as a whole, the only soils that are capable of developing a degree of mesophytism as we know it are those that are very well drained.

In many parts of the temperate regions where subaqueous erosion and deposit have been the rule we are accustomed to find hill slopes deeply gullied, with the surfaces modified by outcrops of bedrock that produce talus accumulations below and coves above. The deformational processes have produced extensive sorting of materials, both vertically and laterally, so that water tables are highly irregular

in their relation to the surfaces. At the same time the rate of leaching and the development of soil profiles have been rendered highly variable from place to place. These are all variations in site, which are reflected in vegetational differences that appear in both vertical and horizontal arrangement.

One of the outstanding features of vegetation on slopes that are highly modified by cryoplanation processes is its lateral and vertical uniformity. Such variety as it possesses is so local and uniformly distributed that its effects are submerged in the mass. Examination of the soils on these slopes shows a very great uniformity in texture and in the position and behavior of the water table. Although the soils may be extremely unstable physically, the instability is so evenly distributed that an aspect of uniformity in the vegetation is maintained. The processes of cryoplanation, then, seem to have a strong tendency to form relatively smooth slopes upon which the sorting of fine and coarse materials is local and of small areal extent.

It is justifiable at this point to ask whether or not these findings in the study of boreal land forms and vegetation are of any immediate use to us who are concerned with problems at or near the glacial boundary. The effects of frost action are quite obviously a function of climate, and it is entirely justifiable for us to assume that climates in front of the advancing and disappearing glaciers were intensely cold. We are justified in looking, therefore, for the effects of this climate and its attendant frost action in the soils and topography in both the glaciated regions and beyond the glacial border. We probably must also insert in our sequence of events in the development of postglacial vegetation a period of time during which there must have been instability of soils and vegetation similar to that now occurring in the Arctic and Subarctic. The length of this period of time is as yet unknown.

Interpretation of our modern vegetation in terms of the periglacial climates should be approached circumspectly, and with full understanding that even in the Arctic where congeliturbation is still active and a major factor, its relation to vegetational dynamics is very imperfectly known.

I have suggested that it is necessary for us to insert in the sequence of postglacial vegetational changes a period of time during which the soils were unstable due to frost action. The cover of vegetation in this period had to be of plants capable of withstanding the instability. We have only small inklings of the floristic character of this vegetation. If we follow the classical interpretation of glacial and postglacial vegetational events we would assume that the plant cover was tundra and composed of arctic species. In this, however, we would be faced with our failure, to date, to find good evidence of an arctic tundra flora at the bases of our American peat profiles. We can get some suggestions, perhaps, by looking at the behavior of modern boreal floras with relation to stable and unstable soils.

The most important division in the boreal vegetation is that between forest and tundra, whether the latter be alpine or on the arctic plain. The timber line is generally regarded as a climatic phenomenon, and its fluctuations are thought to reflect climatic changes. In view of our growing knowledge of boreal soils it is possible to interpret the timber line as a zone of transition from relatively stable to relatively unstable soils, and to look upon the climate as having an indirect effect through its influence upon congeliturbation.

The white spruce, as a species, seems to cross the arctic isotherms at will. It can be found hundreds of miles north of the recognized timber line. Such northward projections, however, are on stream banks and narrow flood plains, or on sandy outwash plains where frost action in the soil is minimal or non-existent. The timber line itself might be thought of, then, as the zone in which the spruce can survive in numbers on the uplands due to the gradual southward amelioration of the extreme instability of the tundra soils. On the other side of the timber line, whether it be southward or at lower elevations on mountain slopes, the spruce fails to survive wherever congeliturbation is unusually intense.

For the majority of species in the boreal flora the timber lines are essentially impassable barriers. When a representative group from the whole flora is mapped, however, it is surprising how many species do cross this barrier with impunity. Of 283 species that I mapped some years ago (Raup, 1947), about 40% proved able to do it. Some of these are arctic species that range as far south as the Great Lakes and New England, while others are forest species that extend into the arctic islands. They must have extraordinarily broad tolerances in their relations to temperature, moisture, photoperiodism, and to instability in the soils. There must be, in any one species population, an abundance of genetic biotypes that gives the aspect of extreme plasticity to the species as a whole.

I believe it safe to say, therefore, that the present flora at nearly any point in boreal America has in it a group of species potentially capable of withstanding the rigors of intensified congeliturbation should the latter occur. Some of these species would be of arctic affinity, but many would be sub-boreal or even north temperate. A point chosen in the tundra west of Hudson Bay would show a high percentage of the former, while one taken in the heavily forested regions farther south would have a preponderance of the latter. Whenever we find soils in the Canadian forest that are actively stirred by frost this proves to be the case, and they are populated by species from the local flora.

I think it not impossible that we now have in the region of the glacial border species whose ranges of tolerance are or were sufficient to allow them to survive the periglacial climate with its attendant instability of soil. They can be looked for among those that are closely related to or identical with species now having wide ranges in the north; or they may have included southern species that had northern biotypes which have since been lost.

These facts and suppositions suggest that the region of the glacial border here in eastern America had no arctic tundra in the strict sense of the term during glacial and postglacial time. It probably had a few alpine plants derived from the pre-Wisconsin alpine floras of the New England mountains and the Adirondacks, and it probably looked like tundra physiognomically; but its predominant species might well have been derived from the native flora.

Dr. Denny in his contribution to this symposium will speak in considerable detail of the evidences of periglacial climates near the drift border. I shall mention only briefly some things that we have seen in central New England and other parts of the Northeast.

A view of the landscape in the neighborhood of the Harvard Forest at Petersham, Massachusetts, particularly if one can be found that is not covered with trees, shows the same broadly rounded slopes and hilltops that are now seen in the Arctic as a result of cryoplanation. These surfaces are characteristic of the upland tills of our region. Dr. Denny will show you the same kinds of surfaces in areas outside the glacial boundary.

When we examine these slopes in detail, we find that their microtopography is composed of broad terraces strongly reminiscent of those seen on arctic slopes (Stout, 1950). Some of them are banked on their fronts by masses of boulders such as one sees now on the alpine slopes of Mt. Washington and throughout the Arctic. The tills and small lenses of outwash within these terraces are found to be bent and involuted in such a way as to prove conclusively that the terraces have been formed by the slumping of masses of material down slope. Many of the terraces have slightly concave surfaces and are so strewn with boulders that they closely resemble the characteristic "block fields" of the arctic and alpine regions. Here and there are rock streams with many of their boulders still on edge, and occasionally one finds well-defined stone rings.

All of our tills in that part of New England are covered with a silt loam which varies considerably in texture and water-holding capacity due to the varying amounts of coarser materials that are incorporated in it. We now believe that the fine materials of this loam were deposited by wind and derived from glacial outwash

plains in the vicinity. They have acquired their coarse materials, stones and boulders, by the same intense frost action that stirred the deeper tills. Evidence for this is to be found in the fact that the loams are worked into the terrace formations along with the underlying tills, and that they show evidence in themselves of the sorting of coarse and fine materials that is seen in arctic soils of similar nature.

It is of interest to carry this study into a still more specific problem (Stout, 1950). On some of our till slopes at the Harvard Forest we have been aware for a long time of peculiar discontinuities in the mixtures of red oak and white ash. There are concentrations of white ash interspersed with other concentrations in which red oak predominates. All of these are growing on lands that were in pasture before 1850. The lands have gone through the white pine stage characteristic of old fields in our area. The pines were logged off in the first and second decades of the present century, and the land is now taken over by hardwoods. We have always assumed that the variation in hardwood types was due in large



FIGURE 5. Ancient stone rings at the base of a slope near sea level in the lower Margaree Valley, Cape Breton Island, N. S.

part to chance. We have thought that the concentrations of white ash were due to the presence in the neighborhood of the old pine stands of old ash trees that supplied an abundance of seed, and that the oak concentrations had a similar explanation. The soils on these slopes have been mapped by the Bureau of Soils as essentially uniform.

We now find that the underlying tills on the slopes are composed of fine materials which are capable of holding up the water table for a considerable part of the growing season. We also find that the overlying loams differ widely in thickness, ranging from depths of 40" to depths of 8". Wherever the distance from the surface down to the fine textured tills is 20" or less, we have concentrations of white ash. If the distance is more than 20", we have concentrations of red oak. When we examine the distribution of the relative thickness of the loams, we find that it is closely correlated with the structure of the cryoplanation terraces. The loams tend to be thickest near the fronts of the terraces, and thin on their upper margins.

From these observations, we come to the tentative conclusion that the present

local distribution of red oak and white ash in this area was determined by the reworking of glacial and wind-blown soils that occurred during the period of instability after the retreat of the last ice.

When we look at any large area of the slope, however, we note a remarkable uniformity in forest type and growth form. This uniformity is the rule rather than the exception in the hill country of New England and the Maritime Provinces. Where breaks occur in it they usually can be laid to human intervention or natural cataclysms. The natural types may change regionally from the central hardwoods of southern New England to the spruce and fir of the North; but within each type, differences that can be correlated with altitude or laterally arranged erosional features are uncommon. The principal variations that one sees are the extreme ones of the alpine zone in the White and Green Mountains, the flood plains of the larger streams such as the Connecticut River, the glacial outwash terraces in the larger valleys, the upland swamps and bogs, and the coastal marshes.



FIGURE 6. An ancient stone stripe and solifluction terrace in a pasture at Petersham, Mass.

I suggest that here again we have a reflection, persisting to modern times and evident in present forest type distribution, of the cryoplanation processes that were most active under the periglacial climate. These processes left the slopes essentially smooth, with soils remarkably uniform in texture, and with water tables that have no great variations in their levels beneath the surface.

Needless to say, a generalization such as this, if it should prove tenable, can have far-reaching repercussions in our future plans for the use of these lands. The silvicultural management of the forests, especially, will be conditioned by it.

I find myself concluding, from observations I have made and such reasoning as I have been able to accomplish with them, that the physiographic ecology of the temperate regions is inadequate for the rationalization of vegetational phenomena in the boreal regions. It appears necessary for us to derive a new kind of vegetational dynamics that will correlate with physiographic processes the chief agent in which is frost rather than running water. I conclude further that though these processes are now largely confined to boreal and alpine regions, they were formerly effective far southward, and at low elevations, even beyond the boundaries of the glacial ice. Their effects here upon soils and surfaces were so extensive

that they still obtain and are strongly reflected in the nature and distribution of our natural vegetation.

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PLEISTOCENE FROST ACTION NEAR THE BORDER OF THE WISCONSIN DRIFT IN PENNSYLVANIA

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The area peripheral to the border of the Wisconsin drift in the Appalachian Plateaus of northcentral Pennsylvania is characterized by an unconsolidated rubble that mantles the landscape from ridge crest to valley bottom. This paper presents the hypothesis that this surficial deposit and the associated landscapes in the periglacial area, or area within a few tens of miles of the Wisconsin drift border, are the result of processes caused by the adjacent Wisconsin ice sheet. In another contribution to this symposium, H. M. Raup describes various phenomena resulting from intense frost action that is characteristic of many parts of arctic and subarctic lands. Soil structures, surficial deposits, and land surfaces found in Potter County and elsewhere in Pennsylvania (figs. 1 and 2) resemble

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those described by Raup from southwestern Yukon and are believed to have had a similar origin.

The topographic development of the Appalachian highlands as pictured in the classical Davisian cycle of erosion proceeded under a "normal" humid temperate climate, and has led to the assumption that the broad, nearly level hilltops have always been the most stable units of the landscape. However, under the hypothesis here presented, the soils on ridge crests near the border of the Wisconsin drift were very unstable during parts of Wisconsin time. The old pre-Wisconsin soils on the uplands that are now preserved only in isolated spots are thought to belong to the Sangamon or last interglacial stage. Therefore it is suggested that these very gently sloping upland surfaces lost most of their ancient soil during Wisconsin time (or possibly in late Sangamon time). Such very gently sloping upland surfaces (slopes of 1° to 5°) are now covered with an unconsolidated mantle of debris that reaches thicknesses of at least 10 feet in places. It is further suggested that this surficial mantle is not forming at the present time but is the result of the breakup of the bedrock by frost action penecontemporaneous with the time when the Wisconsin ice stood at or near its maximum limits in northcentral Pennsylvania. This drift border is believed to be early Wisconsin, possibly Iowan, in age (the "Olean" drift border of MacClintock and Apfel, 1944). The movement of this mantle was due to various causes, the most important of which were solifluction, creep, and running water.

Phenomena indicative of frost action during the Pleistocene have been recognized in Europe for more than three-quarters of a century and have been referred to as periglacial phenomena. An excursion to Spitzbergen in 1910 resulted in a large number of papers by European geologists on frost processes and their products in the Arctic and on the occurrence of frost features of ancient date in the surficial deposits of Europe. Bryan (1928) prepared a review of an extensive work on periglacial phenomena in Europe by Kessler (1925). This review has led to a growing recognition of the importance of frost phenomena for an understanding of the surficial geology of areas near and within the border of the Pleistocene ice sheets.

The literature on the subject of Pleistocene frost action is very extensive. An enlightening summary of the subject together with the extensive bibliography is by H. T. U. Smith (1949b). The March, 1949, number of the *Journal of Geology* (vol. 57, no. 2) is devoted largely to phenomena resulting from frost or periglacial wind action. A recent study by Peltier (1949) deals with similar phenomena in Pennsylvania. Recent work on permafrost or perennially frozen ground especially in Alaska is summarized by Black (1950).

The hypothesis presented here is based on field studies being carried on in Potter County, Pennsylvania, by the U. S. Geological Survey in informal collaboration with the Division of Soil Survey of the U. S. Department of Agriculture and with H. M. Raup and J. C. Goodlett, botanists in Harvard University.

Potter County is near the center of the northern tier of counties along the southern boundary of New York State (fig. 1). The area is in the higher portions of the Appalachian Plateaus and contains the headwaters of the Genesee River that flows northward to Lake Ontario, the Allegheny River that runs westward, and Pine Creek that runs southeastward to the West Branch of the Susquehanna River. The bedrock consists of gently folded sandstone, siltstone, shale, and conglomerate, with very minor amounts of calcareous rock. The regional structure has a northeasterly trend and gives rise to synclinal ridges and anticlinal lowlands with a local relief of 300 to nearly 1000 feet. The highest ridges rise to altitudes of slightly more than 2500 feet. The area is dominantly forested.

About the northern quarter of the county was covered by the Wisconsin ice sheet. The drift border enters the country from the north, near Olean, New York, and has a remarkably straight southeasterly trend across the pronounced ridge and valley topography. The drift border can be rather closely defined as the southern

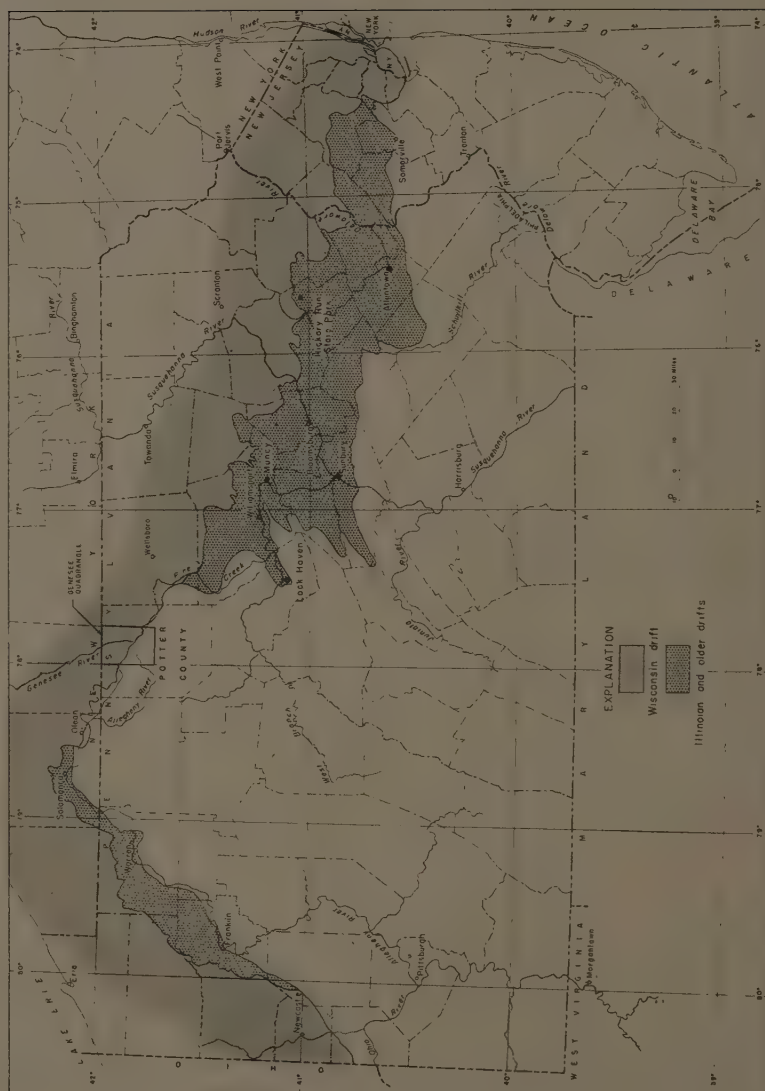


FIGURE 1. Map of glacial deposits in Pennsylvania and adjacent parts of New York and New Jersey. Compiled from Flint and others (1945), Leverett (1934), MacCintock and Apfel (1944), and Salisbury (1902).

limit of erratics of igneous rock or of metamorphic foliates derived either from the Adirondack Mountains or from Canada. There are almost no terminal or recessional moraines and only scanty masses of ground moraine. There are a few small areas of outwash deposits in the form of kame terraces.

SURFACE FEATURES DUE TO FROST ACTION DURING THE WISCONSIN

Blockfields²

Accumulations of large boulders or blocks are found in widely scattered areas near the border of the Wisconsin drift in Pennsylvania. Small blockfields, a few tens to several hundreds of feet in largest dimension, are found in many parts of Potter County and elsewhere. Large blockfields that may be several thousands of feet in length are restricted to areas where the local rock contains beds of massive sandstone or quartzite, as for example, on the mountains south of the West Branch of the Susquehanna River between Muncy and Loch Haven and at the Hickory

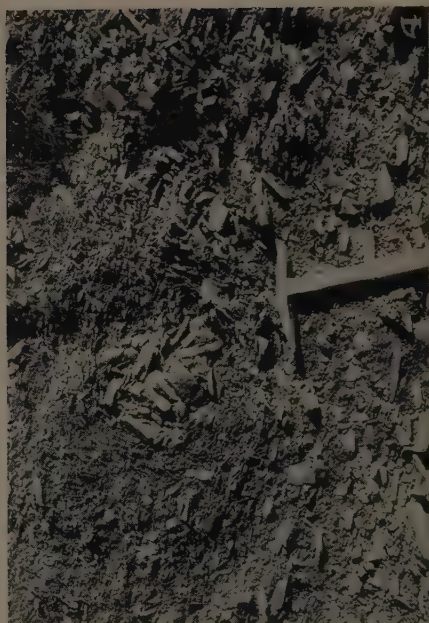


FIGURE 2. Smooth slopes on unconsolidated debris of the Wisconsin stage, from 1 to at least 5 feet thick, developed from shale and sandstone of the Catskill formation. No outcrops of bedrock are visible. Locality is about 6 miles south of the border of the Wisconsin drift. View looking northward from State Highway 144, 0.9 miles west of Germania, Galeton quadrangle, Potter County, Pa.

Run State Park north of Allentown (fig. 1). The blockfields are found on uplands or in shallow valleys where the surface slope is generally only 2° to 5° . The blocks are up to 10 feet in length. Slab-shaped blocks commonly stand with their broad flat surfaces more or less vertical. The individual fragments are covered with lichens and have a weathered rind as much as an inch thick. The blockfields are ancient and do not appear to be forming today. Their antiquity is indicated by the weathered and lichen-covered surface of the individual blocks, the finding of some blocks broken in place into several fragments, the partial covering by vegetation, and their occurrence on very gentle slopes of only 2° to 5° . At only a few localities in Potter County is there positive evidence for present-day movement of individual blocks even on slopes of 25° . This evidence is the disturbance of the surficial organic layer of the soil, either on the forest floor or in the turf of pastures, resulting in breaks in the vegetation on the uphill side of a block or in the formation of a ridge on the downhill side.

The mechanics of formation of blockfields are not clearly understood. There is almost no fine material between the blocks down to depths of 1 to 5 feet. Below that level fine material (generally a silty clay) is present between the blocks. Some workers (Smith, 1949a) argue that a matrix of fine material must have been

²For photographs of blockfields see Smith (1949 a and b).



present between the blocks when they moved. However, in Alaska there are presumably active blockfields in which there is fine material between the boulders at depth, but not within 2 to 4 feet of the surface (D. M. Hopkins, personal communication, December, 1950). The morphological similarity between the blockfields in Pennsylvania and those that are now forming in subarctic and alpine environments leads to the hypothesis that the former are the result of processes active under a cold climate when the surrounding slopes are essentially treeless. It is suggested that such a cold climate was present in the area near the border of the Wisconsin drift at the time when the Wisconsin ice sheet was at or close to its maximum extent.

Surficial deposits outside the border of the Wisconsin drift

The nonglaciated area peripheral to the Wisconsin drift border in Potter County (fig. 1) is characterized by the widespread occurrence of a surficial mangle of unconsolidated debris, largely a rubble. Much of the material is an unsorted, heterogeneous mass that contains from 1 or 2 to almost 100 percent of rock fragments of all sizes from a fraction of an inch to tens of feet in diameter (figs. 3-6). Much of the material on the lower valley walls might be called colluvium. Many of the slab-shaped fragments or flagstones are oriented with their flat surfaces essentially parallel to the slope of the ground. Elsewhere the flagstones may be imbricated with their longest axis dipping toward the top of the slope at angles of a few degrees measured from the ground surface. On ridge tops most rubbles do not show any preferred orientation of the fragments except where the fragments are grouped into circular or linear patterns (boulder rings and boulder stripes). Where the surficial mantle contains considerable fine material and only a subordinate amount of rock fragments, as in areas of fine-grained bedrock such as siltstone or shale, the material resembles till but does not contain erratics or striated rock fragments. The surficial mantle ranges from 1 foot to more than 10 feet in thickness.

It is suggested that this surficial mantle of debris is of Wisconsin age, that it was formed when the ice sheet was at or near the drift border, by processes active in a cold frost climate. On the uplands there is stratigraphic evidence that this mantle has moved down very gentle slopes, 1° to 5° , and in one place accumulated to a thickness of at least 10 feet. The soil profiles developed in the upper part of this mantle suggest that it has been relatively stable for at least 500 to 1000 years. Its degree of weathering is comparable with that on the adjacent Wisconsin drift. The author believes that these deposits can be best explained as the result of processes related to Wisconsin frost action. Most of the deposits on the uplands are probably congeliturbates (Bryan, 1946) or debris produced by frost-riving and

EXPLANATION OF FIGURES

FIGURE 3. Wisconsin colluvium composed of large and small slabs of sandstone with very little matrix and large open voids. Road cut at base of 30° slope on west side of Pine Creek just south of Buckseller Run, Genesee quadrangle, Potter County, Pa.

FIGURE 4. Unconsolidated debris composed of small slabs and chips of sandstone and shale with almost no fines, probably a congeliturbate. Above hammer, fragments show a circular arrangement. Vertical road cut at road corner, about half a mile south of Divide, on southern edge of Laporte quadrangle, Columbia County, Pa.

FIGURE 5. Wisconsin colluvium composed of small slabs of sandstone in a silty matrix. Slabs are rudely imbricated, with their longer axes inclining at a low angle to the left (upslope). Faint irregular stratification visible near base. Exposure in trench that extends upslope across lower end of fanlike deposit. Locality is at mouth of gulch on north side of Allegheny River about 0.4 miles west of Colesburg, Genesee quadrangle, Potter County, Pa.

FIGURE 6. Congeliturbate composed of small slabs and chips of sandstone. Large fragments concentrated in pockets to right of pick and rule. Pockets are cross sections of boulder stripes that extend downslope of 1° or 2° at right angles to exposure. Road bank on north side of State Highway 44 at eastern edge of Oleona quadrangle, Potter County, Pa.

moved by solifluction, the result of a deep seasonal freeze and thaw. The colluvial deposits on the lower slopes are interpreted as the result of a combination of slope wash, creep, and solifluction.

The surficial mantle of unconsolidated debris that essentially conceals the bedrock in areas near the Wisconsin drift border becomes thinner and less continuous as one goes away from the drift border. Likewise there is a change in topography. Slopes in Potter County, for example, have a relatively uniform inclination from top to bottom or become slightly gentler near the base (figs. 2 and 7), and floodplains are essentially absent in headwater areas, the valley walls meeting to form a "V." In contrast in areas farther removed from the Wisconsin drift border the slopes tend to become steeper as one descends, outcrops of bedrock are more abundant, and a narrow floodplain is present even in headwater areas (fig. 7). Such topographic contrasts can be seen in a traverse from Potter County southwestward to Morgantown, West Virginia (fig. 1), or in a traverse from the Wisconsin drift border east of Bloomsburg southwestward for about 75 miles, although in the latter area the presence of scattered patches of pre-Wisconsin drift is a complicating factor. It is suggested that the distribution of this surficial mantle of debris in relation to the Wisconsin drift in Potter County indicates that the two were formed at essentially the same time.

One wonders if the essential absence of gullies on steep cultivated slopes in Potter County as compared with areas more remote from the drift border, such as near Morgantown, is related to the presence of the thick highly permeable rubble in the former area. In Potter County rain water sinks into the ground and emerges as springs near the valley bottom. Near Morgantown, on the other hand, much of the rain water apparently runs off the slope on the ground surface and carves gullies, locally to bedrock.

Boulder rings and boulder stripes³

Many of the surficial deposits of Potter County both within and outside the border of the Wisconsin drift commonly contain a greater abundance of rock fragments at or near the surface than at depth. In many places the fragments form miniature blockfields, surface concentrations of rock fragments from a few inches to 2 or 3 feet in maximum diameter. Locally on slopes of more than 2° these fragments are arranged in stripes or on nearly level surfaces as rings. The bouldery borders are from 2 to 6 feet wide and enclose areas from 4 to 15 feet in diameter with a microrelief of as much as 2 feet. These areas are covered with turf or bushes. Typical boulder rings are most common on poorly drained silty till.

Within the glaciated area the volume of boulders present in any one group of rings is several times greater than that seen in the most bouldery drift in the vicinity. The location of the boulder rings taken in conjunction with what is known of the bedrock indicates that the rings are not related to the outcrop of a given layer of massive sandstone. Boulder rings occur within a few hundred feet of divides and in locations where they cannot be attributed to stream action. Apparently the boulder rings represent a concentration of boulders derived from the reworking of a considerable mass of till. In some places, both within and outside the glaciated area, surficial concentrations of boulders on slopes of 2° to 10° are arranged in roughly parallel stripes. Irregular boulder bands 2 or 3 feet to more than 10 feet wide are separated by relatively stone-free areas 10 to 50 feet wide. Excavations across these stripes show a mass of rock fragments that are packed tightly together and extend to depths of 2 to 3 feet. At comparable depths the material between the stripes is relatively free of rock fragments. Many of the fragments in the stripes are small slabs or flagstones with their broad flat surfaces dipping steeply into the ground and oriented down slope. The boulder

³For photographs of boulder rings and boulder stripes see, for ancient examples, Antevs (1932), Goldthwait (1940), Smith (1949a and b); for modern forms see Antevs (1932), Denny (1940), Rozanski (1943), Sharp (1942), Troll (1944).

stripes are interpreted as the result of the downslope movement of material by solifluction from the surrounding slopes. The boulders move very slowly down the gentle slopes, whereas the finer material (pebbles, sand, silt, and clay) is carried much more rapidly down valley to the principal streams.

The boulders of the rings and stripes are lichen-covered, have weathered rinds as much as 0.25 inch thick, and appear to be similar in general aspect to comparable rock fragments in the weathered zone of the glacial drift in the vicinity.

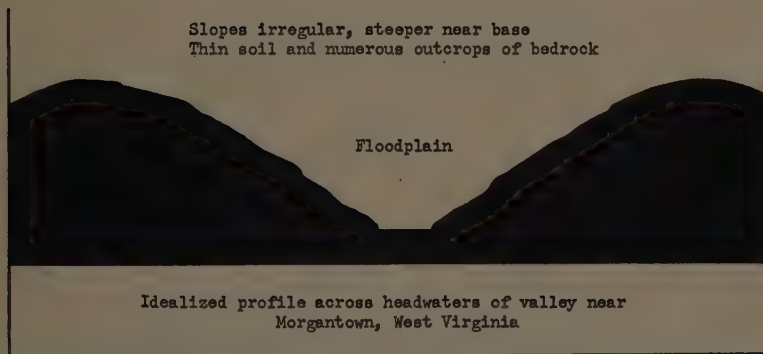
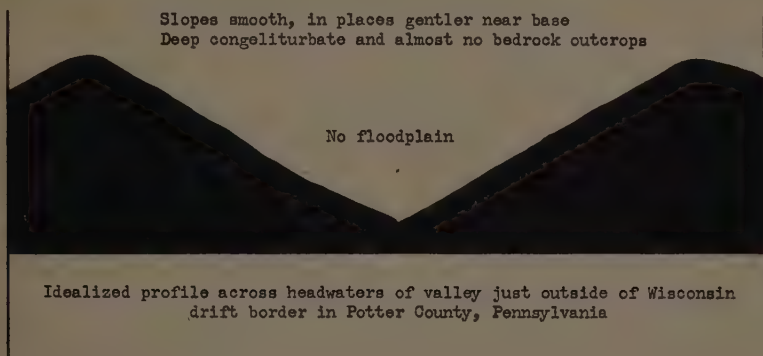


FIGURE 7. Idealized profiles across headwaters of nonglaciaded valleys in Potter County, Pa., and near Morgantown, W. Va.

Many boulders are broken up in place. Several fragments can be fitted together to make a large boulder. All the boulder rings and stripes were forest-covered prior to 1800. The boulder rings are therefore fairly old, probably of early Wisconsin time. Present-day weathering is tending to break up the individual boulders rather than to form new rings.

The morphological similarity between these ancient boulder rings and boulder stripes and those now forming in the subarctic suggests that the two have a common origin. Observations by many workers seem rather definitely to establish the

fact that such soil structures are restricted "to arctic, subarctic, and alpine environments, where the subsoil is for the most part perennially frozen and the surficial layer subjected to repeated freeze and thaw. . . ." (Sharp, 1942). There is as yet not complete agreement as to the actual mechanism involved. Therefore it is suggested that the boulder rings and boulder stripes in Pennsylvania are also the result of a period of deep seasonal freeze and thaw in early Wisconsin time. The boulder rings, stripes, and miniature blockfields are rarely more than one or two boulders deep, a fact suggesting that the assumed freeze and thaw need have extended to only moderate depths, on the order of 10 feet. Perennially frozen ground need not have been present.

CLIMATE AND VEGETATION OF THE PERIGLACIAL AREA

The foregoing hypothesis leads to several tentative conclusions as to the climate and vegetation of the periglacial area. The geographic extent of the surficial mantle of debris suggests that it is related in time and space to the Wisconsin drift in Potter County that is thought to be early Wisconsin, possibly Iowan, in age. The boulder rings, boulder stripes, and blockfields attest to a certain amount of frost action, certainly more than is going on at present. In the absence of any stratigraphic evidence to the contrary it is further suggested that the surficial mantle of debris was formed penecontemporaneous with the above-mentioned soil structures. Therefore it is suggested that both these structures and the associated deposits were formed at a time of more intense frost action. Some of these deposits are interpreted as congeliturbates or debris produced and moved by frost action, especially those on gentle slopes of the uplands. Other deposits, notably those on lower slopes near the valley bottoms, suggest a colluvial origin involving transport both by running water and by mass movements. Such data as are available in the vegetation and the soil profiles indicate that this unconsolidated mantle of debris is essentially stable at present. Rarely are slopes gullied; rain water flows through the surficial deposits rather than on top of them. The writer wonders if it is not possible that the erosion of such permeable materials will proceed at a very slow rate until sufficient time has elapsed for the development of a relatively deep soil profile with a B horizon that contains considerably more clay than is present in the modern soil. To produce the movement of such materials on gentle slopes appears to require a deep freezing and thawing of the ground and the lack of a dense forest cover such as was present here prior to 1800. Although it cannot be detailed here, the evidence is good that in favorable localities the present frost climate is sufficient to maintain a miniature blockfield or to produce miniature boulder rings if the vegetative cover is removed.

The boulder rings and boulder stripes suggest that the depth of freeze and thaw was as much as 6 feet. This is the maximum depth at which the base of the soil structures has been observed in places where there has been apparently no burial by later deposits. It is probable that the ground was frozen for several feet below the base of these structures in order to keep the thawed ground saturated with water. If the ground at the base of these structures was not frozen then water from melting ground ice would flow to greater depths and the fine material of the soil structures would dry and be less subject to frost heaving. It is entirely possible that in places the ground remained frozen at depth for many years, that is to say, that there were areas of permafrost (Muller, 1945) or perennially frozen ground. However, none of the periglacial phenomena seen in Pennsylvania to date furnish unequivocal proof of the presence of permafrost. The above-mentioned soil structures can be explained as the result of a deep seasonal freeze and thaw.

Areas in the subarctic or in high mountains where boulder rings, blockfields, and congeliturbates, or debris moved by solifluction, are actively forming at the present time are all essentially treeless. In Alaska if trees are present at all they are limited to scattered spruce and poplar (*Populus tremuloides*) that are inter-

spersed between areas of active blockfields, boulder rings, or boulder stripes (R. S. Sigafoos, personal communication, December, 1950). Observations in the Yukon (Denny and Sticht, 1950) suggest that most congeliturbation and related frost processes take place in areas devoid of forests. By analogy, when such periglacial phenomena were actively forming on the uplands of Pennsylvania those uplands were likewise essentially devoid of forests.

Blockfields and thick surficial deposits resembling those in Potter County are found in the higher parts of the Appalachian highlands as far south as the Great Smoky Mountains. It seems probable that such features are also of Wisconsin age, and may have been formed at a time when the summits of the highlands were essentially treeless.

There is abundant evidence that eolian phenomena, such as loess, sand dunes, and ventifacts, formed by off-ice winds, are associated with areas peripheral to ice sheets. Such features are beyond the scope of this paper.

CONCLUSIONS

The hypothesis is presented that the area peripheral to the Wisconsin ice sheet in northcentral Pennsylvania contains deposits and soil structures that were formed penecontemporaneous with the adjacent early Wisconsin (Iowan ?) drift. These features are best explained as due to processes related to more intense frost action than is going on at present at a time when the forest vegetation was greatly restricted. This periglacial area probably had an annual depth of frost penetration somewhat greater than at present, but conclusive proof that the ground was ever perennially frozen is lacking.

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THE FOSSIL RECORD NEAR THE GLACIAL BORDER

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The fossils of plants and animals found along the ancient borders of continental ice sheets have long attracted the attention of scientists and discerning laymen alike. As a result of this interest specimens have accumulated in museums and in private collections, and descriptions appeared in scientific journals as well as in magazines intended for the general reader. About a year ago Deevey (1949) reviewed the voluminous literature on Pleistocene fossils and in a long paper gave a critical evaluation of their indicator value. Likewise, Flint (1948) devoted a chapter in his book to the life along the periphery of ice caps and to migration phenomena. If nothing new by way of fossil records as such can be presented in the contribution to this symposium, some unique similarities in migration patterns between northern plants and animals will be shown. An effort will also be made to focus attention on the association of plants and animals of Pleistocene times, which operated similarly to that of plants and animals of to-day.

In a quest for understanding of the vanished more recent life, and in our effort to know its advent and understand its behavior, we soon find ourselves involved in more and more remote history, and we are forced to follow faint trails, and we place the prefix "paleo" before the title of men working in such fields. Workers in paleontology soon learn from the most threadbare fossil records of past life that change, variation, replacement or extinction marked life associations even before man became a part of the environment of that great plant and animal life of the past. Fossil records of the Pleistocene epoch range from massive tusks and skeletons of mastodons to pollen grains and spores as minute as ten microns in diameter. These fossils are the scattered pieces which we are to fit into that great jigsaw puzzle which represents in part the life of the great Ice Age. In such work we cannot escape the obligation to recognize and to show the relationship between life of to-day and that of yesterday.

In the present assignment our task is made easier because we have a great obliteration as the starting point; glaciers left a clean slate, the exposed land became a new habitat to be occupied by plant and animals of that specific time. We also have with us the remnants of that great glacial activity as an object lesson on behavior of ice caps, and on how sharply defined southward extensions of range of certain characteristic northern species of plants and animals can be.

The literature does not lack philosophical treatments of the conditions which should have prevailed at the borders of Pleistocene ice masses. Some pictured the Pleistocene as an immense mass of ice bordering on a rather sunny, balmy south with its characteristic fauna and flora. Pleistocene fossils, however, do not well fit into such a picture, they demand a more extensive range of influence on the climate below the border of the ice caps.

My own studies of Pleistocene and post-Pleistocene times deal almost entirely with forest history. It is, however, desirable in the present discussion that records of lower life as well as of higher animals be included. In this way we will more easily be able to show how plants and animals then as now formed a great interlinked biome, and had similar response to environmental conditions as plants and animals of to-day. As we piece together the several records, as already stated, we cannot escape the conclusion that the great ice masses influenced climate great distances below the border itself. Some of these may have been changes in the extremes (we ecologists are still inclined to evaluate effects on the basis of general climatic

conditions instead of in terms of the control by extremes), some of them may have been the indirect result of microclimatic factors, such as the effect of cold water flowing southward from melting ice. If the polar front line, where the "highs" are developed, was pushed farther south of its present location, and if the highs did not pass into the Atlantic over the St. Lawrence valley, as now, it would also mean that more cold waves would swing southward into Texas and Florida during the course of a year. Huntington and Visser (1922) say, "When the ice sheet had become very extensive, the track would be crowded relatively near to the northern margin of the trade wind belt." They also express the view that a snow field is likely to be an area of high pressure at all seasons. Even though we do not assume such great modifications of the macroclimate, smaller areas, as microclimatic islands, could and very likely did exist. The Mississippi and the Atlantic coastal waters were no doubt much colder than now, and so they would have been microclimatic habitats suitable for occupation by northern plants and animals. Salisbury, as quoted by Baker (1930), sums up the whole situation well by saying, "The great changes in the physical processes which this oncoming of the ice-sheets brought into operation effected corresponding changes in life and in the processes which depend on life. In the first place, the total amount of land life must have been greatly reduced. If account be taken of mountain glaciation in both hemispheres, as well as of the ice sheets, it is probably within the limit of truth to say that conditions became so far inhospitable as nearly to eliminate land life from about 1/7 of the land of the globe, and to have rendered conditions relatively inhospitable over a still larger area. The crowding of land life off eight million square miles, more or less, must have tended to concentrate it upon the land which still remained hospitable, and to decimate or exterminate those forms which could not migrate readily." Fossil remains indicate that conditions for which migration had no solution were also involved. In amazement one asks, "Why were so many, if not most, of the native large mammals exterminated during or soon after Pleistocene times?" Among these are all native horses and camels, six species of elephants, the giant sloth, various species of moose and elk, and the giant beaver. We may never find an answer to this question.

Distribution maps of these large Pleistocene mammals indicate four more or less climatically controlled groups. One was distinctly southern, another was primarily northern (figs. 1 and 2); then there was a group which appears to have been intermediate, and finally, one group seemed to be so cosmopolitan (*Elephas colombi*, and *E. imperator*) that very little climatic control can be read into their distribution pattern. Hay (1922, 1924) is of the opinion that zones, determined by temperature, existed during the glacial period the same as now. Distribution maps support such an assumption fully. In figures 1 and 2 are presented a selected list from Hay (1922, 1924) and Lyon (1936) which are considered as mammals typical of cold climates. We note that the greatest concentration of these fossils is in areas which were the border, or near border, of the Wisconsin ice sheet. The distribution further shows that ranges extended into regions which appear to have been out of their macroclimatic range requirements. We have such unusual distribution patterns of northern plants and animals to-day. The extraneous distribution is recognized as being due to microclimatic factors operating in what we call "relic colonies." These may, indeed, be extensions into rather than remains of a former general distribution. The significance would be the same. No doubt isolated spots within the borders of an otherwise inhospitable climate existed also during Pleistocene times. This should find support by presence of microscopic water life as well as by fossils of typically northern higher plants and animals, and their correlation in distribution ranges.

Let us first look at the records of microfossils, such as diatoms, found in peat. Hanna (1923-24, 1933) studied sediments from both central and northern Florida (fig. 2, C) and he found an assemblage of species whose present range is distinctly

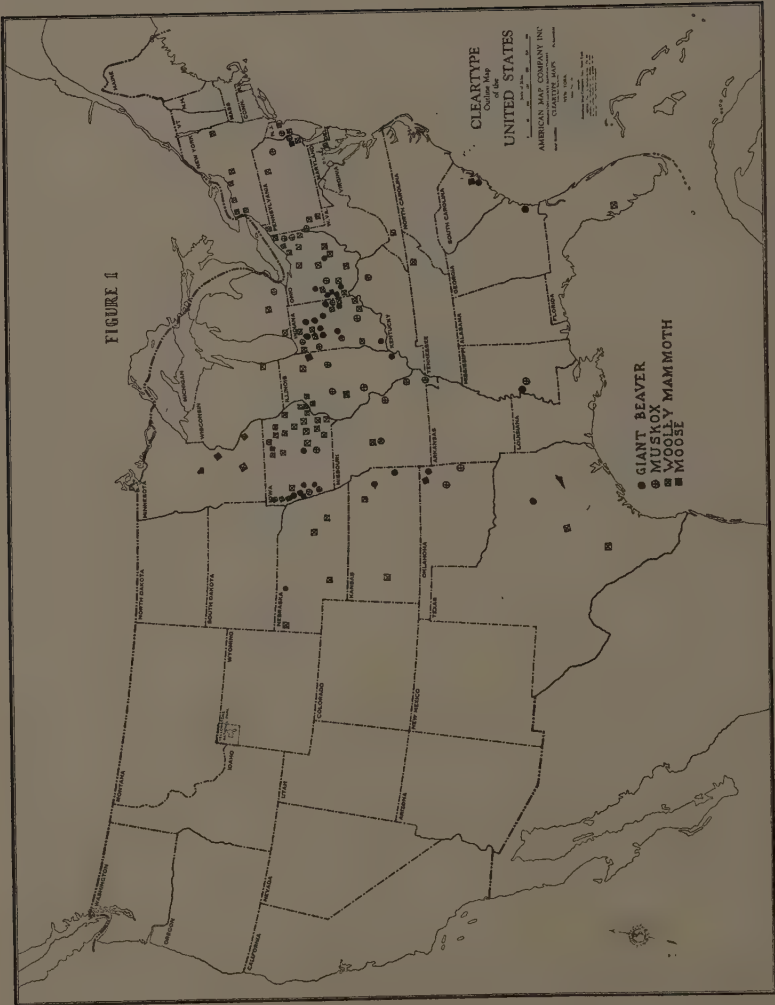


FIGURE 1. Geographical distribution of fossil records of arctic and subarctic animals.

northern, New England and Canada as well as bogs of the Lakes States. Most of the diatoms were very abundant. He lists *Navicula serians*, *Eunotia diodon*, *E. flexuosa*, *E. robusta*, *Neidium iridis*, *Pinnularia interrupta*, *P. legumen*, *P. major*, *P. nobilis*, *Suritella oblonga* and *Cyclotella striata*. Patrick (1946) did not find so abundant a collection of northern diatoms in the Patschke Bog in Texas but she did find *Pinnularia divergentissima*, a northern or alpine species. Davis (1946) voices doubt about the indicator value of diatoms for colder climate in Florida during Pleistocene times; he however readily reads colder climate into fossil pollen of spruce and fir from peats of Florida (fig. 2,B). Let us now briefly review the records of typically northern trees in southern latitudes. Frey (1950) reports from coastal plain lakes of North Carolina (fig. 2,A) up to 6 percent pollen of *Picea*, and scattered grains of *Abies*. At the 14¼ foot-level pollens present were: Pine 89.6, spruce 5.8 percent and oak only 3.1. Spruce was consistently present from the 21-foot to the 12¼-foot levels, where it disappeared from the profile. Davis (1946) quotes L. R. Wilson as having found pollens of spruce and fir in Florida peats (fig. 2,B). Potzger and Tharp (1947) report up to 4 percent white spruce, black spruce and fir pollens from the lower levels of the Patschke Bog in Lee County, Texas (fig. 2,E). Fisk, Richards, Brown, and Steere (1938) described the following macrofossils present in peat from the East Baton Rouge Parishes in Louisiana (fig. 2,D): Four species of northern gastropods, cones of tamarack and white spruce, twigs of *Thuja occidentalis*, and two northern mosses, *Amblystegium Juratzkanum* and *Taxiphyllum geophilum*.

Before us are the fossil evidences of spruce and fir as well as other northern plants in North Carolina, Florida, Louisiana and Texas (fig. 2,A-E) and overlapping this range of plants are fossil records of musk oxen, woolly mammoth, elk, reindeer, and others. Their greatest abundance is near ancient glacial borders; they show up sparsely in regions now typically northern (Michigan, Wisconsin, Minnesota) but leave faint trails down the Atlantic coastal areas and the Mississippi basin. It is difficult to interpret such distribution patterns of a great biome of plants and animals whose normal range is northern without assuming cooler climate in those states, microclimatically at least, than that found there to-day. The abundant records of these mammals near the border of the Cary substage of Wisconsin glaciation, and meagre presence to the north of it suggests ice barriers preventing northward migration to border mammal life, and extinction for most of them before the region became free of ice.

But enough of the spectacular southward extension of cool or cold climate plants and animals, which give every evidence of having been a great biome. We will now turn our attention to border areas and see what information fossils can give us about life in such locations. Baker (1930) expresses as his opinion about life at glacial borders as follows, "It is apparently in accord with the ascertained facts, as indicated by the fossil remains found between the till sheets listed in this work, to believe that at each interglacial interval there was first a migration northward into territory laid bare by the retreating ice and later a southward migration as the climate changes with the on-coming of the new glaciation . . . the effect of such migrations has been to cause the extinction of many species of insects and mammals while causing little change in plants and mollusks." He lists from near border areas 145 species of plants, 298 mollusks, 4 crustaceans, 108 insects, 3 fishes, 1 amphibian, 6 reptiles, and 117 mammals. A total of 540 animals and 145 plants. Of the animals 104 species of insects and 87 mammals are extinct. Among the plants present were such common present day species as: *Chara*, *Equisetum sylvaticum*, *E. fluviatile*, *E. scirpoides*, *Lycopodium selago*, *Taxus canadensis*, *T. minor*, *Pinus strobus*, *Thuja occidentalis*, *Larix*, *Juniperus virginiana*, *Abies balsamea*, *Typha latifolia*, *Potamogeton*, *Carex*, and *Scirpus*. From the Pleistocene of Minnesota Rosendahl (1948) brings a long list of macrofossils of plant species collected from soil deposits. While the absolute placement with respect to border

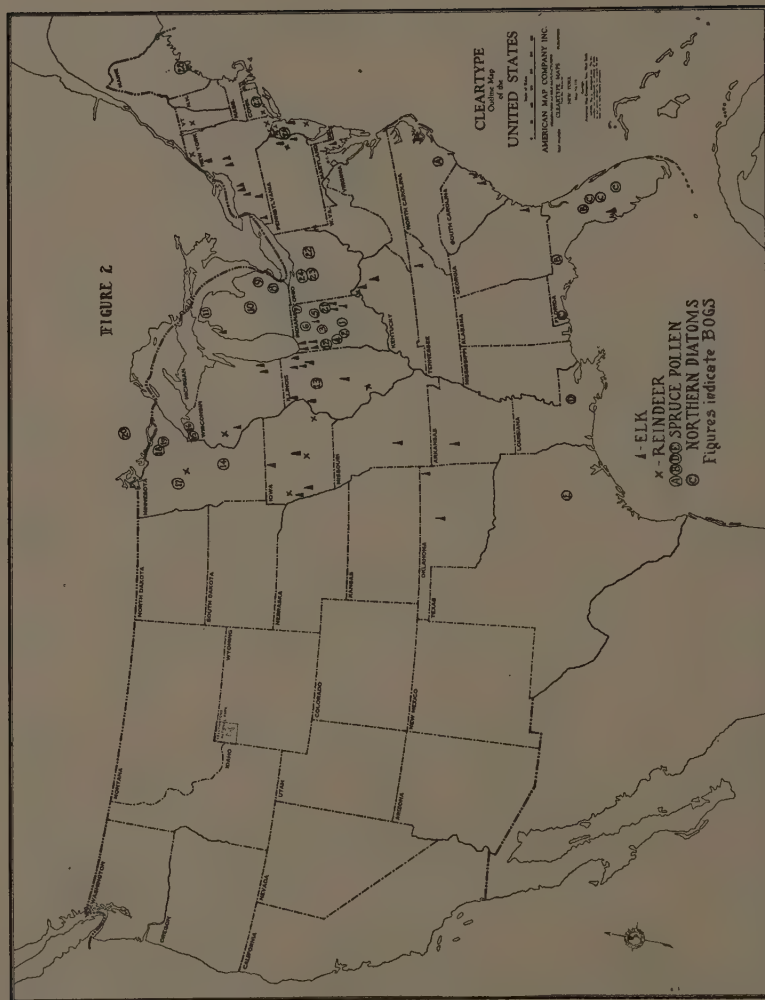


FIGURE 2. Geographical distribution of fossil records of extinct arctic and subarctic animals; locations of peat deposits where pollens, cones, twigs of northern trees, diatoms and mosses with characteristic northern ranges were found. Figures within circles show locations of bogs from which records shown in figure 3 were taken.

areas cannot well be determined from the above two sources of information, they must have been close enough to come under the influence of the ice sheets.

From more definite location near border areas we have two sources of information, i.e., buried organic deposits and peat from bogs and present-day lakes. Records from lakes are perhaps the most reliable for complete profiles because fire has not influenced the organic deposits. There is, however, the old, old question, "Did tundra border the ice sheets of Pleistocene times?" The pollen analysis records are disturbingly silent on this question. There are a few records, one by Potzger and Friesner (1948) from a bog in Maine, where grasses are remarkably abundant. However, one misses *Salix* and *Alnus* which Cooper and Lawrence report as the most common first invaders at glacial borders. One thing is certain, the lakes were formed by the glaciers, but as Deevey (1949) points out, we have no

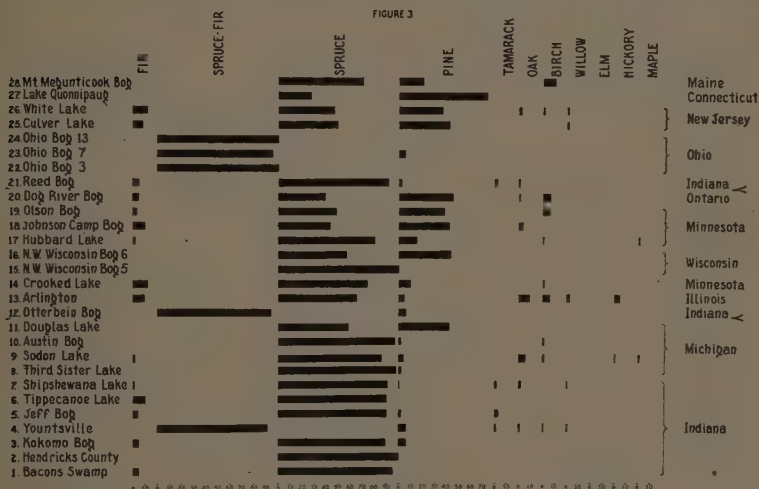


FIGURE 3. Pollen counts from lowest levels of 28 bogs showing composition of forests along the borders of Wisconsin glaciation.

assurance that the depressions were not ice-filled for a long period of time after glacial retreat, in that case the early vegetational history may be wanting. In most bogs and lakes which the writer studied vegetation begins with pollens of forest trees.

First let us look at life as it was reported from buried soils representative of various interglacial stages. Cooper and Foot (1932) discovered a buried soil layer in Minneapolis. In their opinion it was a pond, filling in while glaciers were still within the borders of Minnesota. Records of life included mollusks, ostracoda, the mosses *Drapanocladus fluitans submersus*, *D. minnesotensis*, *Calliergon giganteum*, *Neo-calliergon integrifolium*, and various species of trees. Associated in the tree stratum were *Larix*, *Picea mariana*, *Picea glauca*, *Abies*, *Pinus strobus*, *Betula papyrifera*. In the same state Nielsen (1935) found the following plant remains in a soil layer which he calls pre-Kansan: *Abies*, *Picea*, *Larix*, *Betula*, *Acer rubrum*, *Juglans* or *Carya*, *Prunus*, *Lycopodium complanatum*, *L. lucidulum*. From the Two Creeks forest bed layer in Wisconsin, Wilson (1932) reports: *Bryum binum*, *Calliergon turgescens*, *Camptothecium nitens*, *Campylium stellatum*, *Ditrichum flexicaule*, *Drapanocladus revolvens*, var. *intermedium*, *Scorpidium scorpioides*,

Swartzia montana, *Bryum cyclophyllum*, various grasses, heaths, ferns, and the bracket fungus *Polyporus*. In addition he listed the mollusks *Fassoria dalli*, *Pupilla muscorum* and *Succinea avara*. Among the trees were named spruce, birch, jack pine. While here, again, we have no evidence that these buried soils were laid down while glaciers stood by, we do recognize the plants as northern and in some cases they are species which crowd to the borders of glaciers to-day.

In conclusion let us briefly consider some pollen profiles from bogs and lakes. They have been arranged more or less in three series (fig. 3). With Indiana as the starting point, they radiate towards three different directions. Only the lowest foot-level is given with the assumption that this level marks the time when glaciers had not removed far from the region, perhaps only a few miles. It is unfortunate that lakes and bogs are obliterated in areas of Illinoian glaciation, at least in Indiana, but we have abundant records from Early Wisconsin (Tazewell substage) and Late Wisconsin (Cary substage) bogs. In my own studies there is no clear picture to show how interglacial periods influenced forest succession. This is true even for the physiographically clearly defined Cary substage where it borders on the earlier Tazewell. There is little indication in areas of the Tazewell substage in Indiana that moderating climate had influenced succession of forests. The bogs from the two areas show a merging into a continuous spruce-fir period for these substages. The only clearly defined division between the two substages are the greater number of foot-levels showing spruce-fir forest type in the Tazewell than in any of the bogs and lakes from Cary locations, and later absence of the pronounced pine period in Tazewell locations which shows up prominently in bogs located in Cary drift.

The work of many investigators was included in the list of bogs shown in figure 3. Correlating authors' names with numerical designation of the bogs in figure 3, they are as follows: 1. Otto (1938), 2. Potzger (1943), 3. Howell (1938), 4. Swickard (1941), 5. Keller (1943), 6. Potzger and Wilson (1941), 7. Keller (1943), 8. Potzger and Wilson (1941), 9. Cain and Slater (1948), 10. Potzger (1948), 11. Wilson and Potzger (1943), 12. Richards (1938), 13. Voss (1937), 14. Wilson and Potzger (1943a), 15. Wilson (1938), 16. Wilson, (1938), 17. Potzger (1946), 18. Potzger (Ms.), 19. Potzger (Ms.), 20. Potzger (Ms.), 21. Griffin (1950), 22. Potter (1947), 23. Potter (1947), 24. Potter (1947), 25. Potzger and Otto (1943), 26. Potzger and Otto (1943), 27. Deevey (1939), 28. Potzger and Friesner (1948).

By way of summary we can state that the most important pioneer tree, as shown by all bogs (fig. 3), was *Picea*. In some instances it had no associates, at other locations *Abies* was an associate. In the Great Lakes area and in the Atlantic coastal regions pine was an early invader with spruce and fir. However, even such broad-leaved genera as oaks, hickories and maples were isolated early invaders in some regions (fig. 3). As a whole, the pioneer forest was simple in sociology and very similar in composition to that bordering on continental North American ice caps to-day. These modern pioneer forests have been described by Cooper (1939), Griggs (1934), and Marr (1948), so that their sociology is known.

It seems that the general pattern of life associations near the border of Pleistocene ice caps located on land masses which have uninterrupted extension for great distances southward were similar to those we meet in the Arctic to-day. Genera, perhaps even species, of forest trees were the same as those near glacial borders in North America at present. The pioneers then were largely spruce and fir and they still are the most important genera. The fossil evidence when linked with life of to-day shows that since the day when ice caps slowly wasted the spruce and fir, the Jack pine and paper birch, the muskox, reindeer, elk, and moose have moved northward in the shift of climatic belts as plant and animal associations of arctic and subarctic habitats.

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THE POSSIBLE ROLE OF MICROCLIMATE¹

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Since the publication of Geiger's (1927) pioneer systematic treatment of microclimates, there have been important advances in this phase of climatology. Many of these studies are of more than passing significance to plant ecology, as a perusal of Geiger's (1950) second revision of his earlier work will reveal. Research during the past quarter-century has resulted, among other things, in giving *dimensions* to microclimates and microclimatic situations. It has changed the word *microclimate* from a philosophical term to one that refers to real, and to a greater extent than ever before, measurable conditions. The old term, by implication at least, was used to answer all questions, some of them unanswerable; the new concept raises more questions and answers fewer, but gives promise of more fruitful results in ecological investigations.

Over almost all landscapes, just above the substrate, there is a mosaic of varying weather regimes. The pattern may be simple, as over a level plain, or it may be exceedingly complex, as in mountainous country. A dozen strikingly dissimilar weather regimes have been described within a single small valley in the dissected

TABLE 1. *A Comparison of Certain Climatic Data Obtained in a Grotto and Frost Pocket, with nearby Weather Bureau Records. Data from a single year.*

	Grotto	Frost Pocket	Weather Bureau
Longest frost-free period in year....	276	124	160
Longest frost period in year (hrs.)..	373	246	
Minimum temperature (year).....	+14	-25	-18
Maximum temperature (year).....	75	93	102
Date last spring frost.....	3/9	5/25	4/22
Date last fall frost.....	11/29	9/25	9/29
Rel. rate of evaporation (per season)	1	5	
Precipitation (inches).....	00.0	41.0 [±]	41.0

Appalachian Plateau (Wolfe, Warcham, and Scofield, 1949). Valley heads (coves), grottoes, variously-exposed slopes, ridges, crevices, valley bottoms, and other sites, all have differing weather regimes at all seasons. In table 1 certain data from two microclimatic situations in this valley, are compared with macroclimatic conditions.

Detailed analyses of microclimates have been published elsewhere (Geiger, 1950; Wolfe, Warcham, Scofield, 1949) and are beyond the scope of this paper. However, two or three aspects of the data in table 1 may be mentioned to illustrate the role that microclimates might play in the interpretation of floristic phenomena.

The data indicate that the longest frost free period in the plateau occurs in grottoes under present climatic conditions; moreover, extreme minimum temperatures are nearly 40 degrees higher than the lowest temperatures elsewhere. Even though it is assumed that glaciation had pronounced effects on periglacial macroclimate, extremes in these sites might well have been within the ecological amplitude of many boreal, as well as southern species. Not only is the frostless season longer in grottoes than elsewhere, but also the frost season, a condition favorable to many species of higher latitudes that require periods of varying duration to cold before breaking dormancy. It is these kinds of phenomena that make up the warp and

¹Department publication 522.

the weft of our point of view with regard to the role of microclimates in the interpretation of periglacial conditions in the Ohio region.

Whatever the source, and whatever the nature of biota forced into the Ohio region during the Pleistocene, some extraneous species of both plants and animals have persisted in certain of these microclimates since the last glacial retreat. Presently the question as to just where these relicts were during the various maximum advances of the ice will be considered.

VARIATIONS IN MACRO-PERIGLACIAL CONDITIONS

Because of fundamental differences in general physiography and macroclimate, microclimatic, pedologic, and biotic phenomena and conditions along the ice border must have varied considerably from Long Island to the Rocky Mountain front during any single ice advance and from stage to stage during the Pleistocene. In the Ohio-West Virginia-Kentucky region, for example, the first ice advance (pre-Illinoian?) blocked the great Teays drainage system forming a vast proglacial lake, fingers of which extended far southward into tributary valleys in Kentucky and West Virginia (Transeau, 1941; Wolfe, 1940). This phenomenon must have had marked effects on climate and soils and consequently biota. Moreover these conditions would be greatly different from periglacial conditions elsewhere, *i.e.* on the coastal plain, in the Appalachian mountains, and the central lowlands. The discussion immediately hereafter is based on evidences collected in the Appalachian Plateau region.

ARRIVAL OF RELICT BIOTA IN THE PERIGLACIAL REGION

The borders of ice sheets in the Ohio area lie wholly in a Deciduous Forest climate. Within the area, however, are numerous relict communities and disjunctive species as well as species from other formations at the edge of their range.

During the 60 million years preceding the Pleistocene, the vast Teays drainage system developed. With headwaters in the southern Appalachians, and with its confluence with lake or river somewhere in the upper Mississippi Valley, its valley walls and bluffs and its flood plains formed continuous habitats, which along with the tremendous propagule-carrying potential of the system itself, resulted in an exchange of biota, north to south and south to north.

With the advance of Pleistocene ice, a northern biota invaded the area. Whether or not it invaded and passed on, returning later, or whether it simply invaded, will be considered shortly. At any rate, certain of these northern species, along with southern species, occur today in special microclimates within a few miles of the glacial border. For example, in a small re-entrant (grotto) in the cliffs at Old Man's Cave in Hocking County, Ohio, is *Sullivantia sullivantii*, separated by 600 miles from its nearest relative northward in the Dells of the Wisconsin River. With it is *Silene rotundifolia*, a southern Appalachian species at the northern edge of its range. Irrelevant to the present thesis, but none-the-less interesting, is the presence in the same grotto of *Dodocatheon meadia*, of the Prairie.

Briefly, two basic points have been made:

1. There is a multiplicity of climatic regimes today in the plateau region near the glacial border.

2. Growing together in these microclimates at the present time are both species with northern affinities and species with southern affinities, along with various others of no importance in the present discussion.

With the advance of ice at any time during the Pleistocene, migrations of these two floras were limited to the following:

1. Southern species at the northern edge of their range either retreated to the south, returning in post-Pleistocene time to the habitats they occupy today; or, they remained in the periglacial area (not necessarily in the same location) through the ice age.

2. Northern species either became established in the periglacial region during the ice age, or migrated on southward, returning to their present sites at some post-glacial time.

SULLIVANTIA AND SILENE

Many species of plants of the southern Appalachians are at the northern edge of their range in southern Ohio and likewise, an even greater number of species of the Hemlock-Hardwood Formation are at the southern edge of their range or disjunctive in southern Ohio, facts recognized early in the century by Griggs (1913). The two species used to illustrate this discussion were chosen because they occur in special microclimates from which more data have been obtained than from many others just as distinctive.

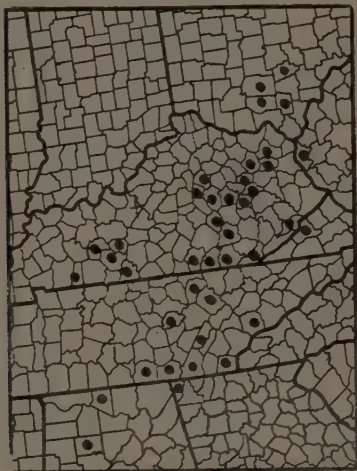


FIGURE 1. Distribution of *Silene rotundifolia* Nutt.

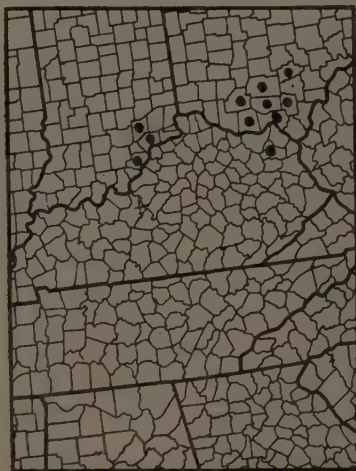


FIGURE 2. Distribution of *Sullivantia sullivantii* (T. & G.) Britt.

Sullivantia is known only from southern Ohio, southern Indiana, and northern Kentucky (fig. 2). It is confined to limestone and sandstone cliff faces, usually on ledges or in grottoes that are moist, yet relatively well-lighted. It produces abundant seed, but at present nothing is known by this writer of its viability.

Silene occurs locally through the southern Appalachians (and rarely to the west of the plateau), reaching its northern limit in several stations in southern Ohio (fig. 1). It too is confined to grottoes, crevices, and ledges that develop in vertical limestone and sandstone cliffs. Superficially its habitat may appear drier than that of *Sullivantia*, but its roots are often long (more than 6 feet) and are always in contact with abundant moisture. It also produces abundant seed from July until November in the Ohio area (Heaslip, 1950), which is almost 100 percent viable.

Both of these species then, are confined to the peculiar grotto-crevice-ledge environment, certain data from which are given in table 1. It is not implied that these measured factors are the ones responsible for the persistence of these species in these situations. Other factors, unmeasured or unmeasurable, may be more important. It can be said that they are confined to a microclimatic complex of which the measured factors are a part, at least.

PERIGLACIAL MICROCLIMATES

With the ice as a stage of maximum advance, the periglacial microclimatic mosaic was altered. Certain complexes were perhaps eliminated, others expanded or contracted, with new ones being added. Indeed, the mosaic of microclimates might well have been simplified, for near the ice border, glacial winds were meeting the Gulf air masses and cloudy, rainy weather must have been a conspicuous feature of the growing season.

At any rate, the grove microclimatic complex must have occurred somewhere near the glacial border. Whether it was more widespread, or localized, as it is today makes no difference. For if we accept the notion that the terrain south of the ice was tundra-like for miles (Deevey, 1949), we will have to assume that both *Silene* and *Sedum* were destroyed in the periglacial region. Expansion of the grove type microclimate could well account for providing conditions favorable to migration southward and preservation in grove refugia there. But any great migration—in terms of several hundred miles, not to mention a Floridian visit (Deevey, 1949)—“with the coming of the tundra”, raises two pertinent questions.

1. If these species retreated far into the southern Appalachians during Pleistocene, how, with their narrow ecological amplitude and lack of continuous migration routes, did they get back near the glacial border?

2. Having once arrived, why did *Sedum* and *Silene* not persist in some of the millions of grove microclimates of the southern mountains?

The realization is clear that one swallow does not make a summer, nor a single catchfly a foundation for interpreting Pleistocene periglacial conditions. But along the glacial border in Ohio is a rather impressive group of southern Appalachian and southern species to which question 1 above, might be applied. Excluding *Polypodium polypodioides* the Gray Polypody, because of its windblown propagules, the list would include *Magnolia macrophylla*, Great-leaved Magnolia; *Pauciflorus nivalis*, Mountain-lower, *Rhododendron maximum*, Great Rhododendron, *Sorbus grandifolia*, Large-leaved Sorus, *Halecia scutellaria*, Silver-bell; *Asclepias*, Flame Anemone, *A. nodiflorum*, pink Anemone, and *Iris versicolor*, Dwarf Iris.

Likewise there are certain northern species occurring in southern Ohio which apparently were present during the ice age. Some of these occur far to the south along the Atlantic seaboard, but the edaphic factor provided the continuous habitat. E. g., exposure of the seacoast with lowering of sea level during Pleistocene, and suitable continuous habitats must have been available in the mountains over which these reached the southern Appalachians.

MICROCLIMATES ON THE COASTAL PLAIN

With a great deal less evidence, one may suggest the possible occurrence of microclimates on the coastal plain proper, these being invaded by propagules of northern species in the time of flood or in some other manner. The existence of “cold pockets” even as far south as New Orleans, is suggested by the data of McDonald (1941) and Dyke (1941). Variations in minimum temperatures as great as 26° are reported between New Orleans and a station six miles away. On 14 occasions in four years, differences greater than 20° were noted. A temporary establishment of northern species in such sites, if flood waters may be assumed to be an efficient propagule-carrying agency is not altogether unreasonable. Earlier mention was made of the probability of abundant rainfall at the ice front when the cold glacial winds came in contact with the warmer Gulf air masses. Scott (1950) has described such conditions in front of the ice cap on the island of Kerguelen, pointing out that rain, sleet or snow falls during 200 to 320 days per year. No such frequency was probable in the plateau region during Pleistocene but considerably greater rainfall than is now recorded must have occurred regularly—especially during the growing seasons.

With increased rainfall at the ice front, plus meltwater from the vast snow and ice fields to the north, in addition to the regular precipitation in mountains to the southeast, tremendous floods must have been characteristic phenomena of the Ohio and Mississippi Valleys in glacial times. These floods were presumably more frequent, and in volume several times as great as the biggest flood of modern times, when a crest of 80 feet was reached at Cincinnati. The propagule-carrying potential of these floods might be exceedingly great, and the dispersal over the flood plains and lowlands of the southern plains relatively widespread.

One other phase of the ice age migrations might be scanned with the above mentioned pluvial conditions in mind, namely that of "the Pleistocene deposits of Louisiana [containing] tulip tree, sweet gum, tupelo, magnolia, along with northern conifers . . ." (Deevey, 1949).

Before agreeing that "the summers in Louisiana [were] cool enough for spruces while the winters were still warm enough for magnolias" (Deevey, 1949), another alternative is suggested. The same flood waters mentioned above, advancing as they must have, through various vegetation belts south of the ice, could well have carried a tremendous load of organic debris. Before interpreting this mixture of magnolia and fir in terms of forest associations, the notion of fossil flotsam might be investigated.

SUMMARY

The preceding discussion has dealt briefly with the possible role of microclimatic phenomena in the interpretation of periglacial biotic and climatic phenomena. To a large extent, the discussion is based solely on microclimatic evidences, and these would seem to support a concept that has glaciation exerting little influence on climate or biota very far beyond the ice front.

A more thorough knowledge of microclimatic phenomena is admittedly needed, as well as a more precise knowledge of floristic geography, before this relatively new discipline can contribute major evidences such as those presently being advanced by the pedologists, geologists, climatologists, and biologists.

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PLANT DISTRIBUTION IN RELATION TO THE GLACIAL BOUNDARY

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A consideration of plant distribution in relation to the glacial boundary involves, first, a knowledge of the present geographic distribution and edaphic requirements of species and communities, and, second, an attempt to interpret these distributions. Opinions may differ as to how extended a latitudinal area should be included, how far to the southward of the glacial boundary distributions were profoundly affected.

In a recent publication, Deevey (1949) has advanced the interesting but surprising thesis that "there has been sufficient time, and sufficient transfiguration of geography, for the pre-Pleistocene distribution pattern to be completely transformed in a very large number of cases." And, as a corollary to this, he states as a *principle* that "all distributions of species are taken to be of Pleistocene date in the absence of good proof that they are older."

I believe that each problem should be approached individually and without any preconceived "principle" concerning date when the pattern of distribution arose. There are few instances where "proof" of interpretations is possible. There is no more possibility of proof of a post-Wisconsin distribution date than of interglacial or preglacial dates, except on the area of Wisconsin drift where late-glacial and postglacial migrations are recorded in pollen diagrams.

In attacking such problems, we must obtain as accurate a picture as possible of present distribution; we must consider the environmental requirements of plants involved—for example, soil and moisture requirements, length of day (for some species require long days to initiate flowering, hence are latitudinally limited southward), and temperature range under which they are now growing naturally. We must, of course, admit the possibility that gradual changes in physiologic requirements have taken place and are taking place. We must realize that many species vary, physiologically if not morphologically, in different parts of their ranges (biotype variability). At the same time, we are justified in assuming that such changes are not of great magnitude; for example, that trees with thin more or less large leaves were mesophytes in the past as they are today, that xerophytes have not become hydro-mesophytes in the last 20,000 years or less.

We must consider events, from the present backward into geologic time as far as present or closely related species may have been living, for, except in the glaciated areas, vegetation earlier than the last ice advance, or even earlier than the onset of the first continental glacier, must be taken into consideration. The land was occupied, and occupying vegetation affects the habitat. We must consider the possible or probable shifts induced by *all* sorts of major environmental changes, physiographic as well as climatic.

All available evidence should be used—fossil evidence, and evidence concerning the environmental conditions of the past. Fossil evidence is very scanty in the unglaciated area. Evidence concerning soil-freezing phenomena is gradually becoming available. Microclimatic studies are suggestive. Chromosome studies are sometimes enlightening.

In a few instances, a genetic approach to problems of distribution has been possible. For discussion of such problems, the literature must be consulted.

Because of time limits, I shall emphasize plants of Appalachian and eastern interior range. I will include not only species occurring near to the glacial boundary, either in isolated stations or more or less generally distributed, but also certain

species farther to the south, whose distributions have generally been conceded to be related to pre-Pleistocene physiographic history, but whose distribution patterns, according to Deevey, are a result of Pleistocene and post-Pleistocene movements.

When we consider species or communities whose ranges are in some way correlated with the glacial boundary—geographically, not necessarily causally—we find that they may be classified readily into groups, as northern, western, and southern.

A considerable number of species, general northward, appear to have a scattered distribution over the southern part of the area of Wisconsin drift, and rarely, if ever, occur south of the Wisconsin glacial boundary, except on the high northern Allegheny Plateau and Allegheny Mountains. A large proportion of plants illustrating this type of distribution are bog plants, which now remain in localized bog communities. Such distribution patterns are generally, and no doubt correctly, explained as due to northward migrations which followed the retreat of continental ice. But, does explaining bog relics as left behind during retreating migration of northern vegetation really explain them? Where did these bog plants spend the last cold period of the Pleistocene? Where, south of the glacial border, and within any reasonable distance of it, could they have found suitable edaphic environment? I consider this an unanswered problem, unless we concede the possibility that they occupied bogs in the detritus on or just within the ice margin. In northern latitudes, bog plants are growing today over permanently frozen subsoil.

Other species, with much the same type of distribution pattern as the bog plants, but with different edaphic requirements, occur in a few isolated stations not far to the south of the glacial boundary. *Taxus canadensis* is one of these, with its southernmost interior station on the bluffs of Tygarts Creek in Carter County, Kentucky, about 50 miles to the south of the glacial boundary, where it is out of accord with the accompanying vegetation (fig. 2). *Acer spicatum*, in a gorge in the same geographic area, has its next nearest station (Clifton Gorge, Greene County, Ohio) within the area of Wisconsin drift (fig. 3). *Thuja* on calcareous cliffs occurs, in the interior, as far south as southern Ohio, and in the Appalachian Valley, as far south as Tennessee. Such local occurrences, often far to the south of the area of general distribution, are related to local habitats affording suitable edaphic environment or, in some instances, protection against too great competition because the habitat is unsuitable to the regional vegetation. There is no evidence that such plants were formerly widespread as far south as these outposts, or, in most instances, that they ever occurred much farther south. Fragments of *Thuja* in Pleistocene deposits along the Mississippi River in Louisiana (Brown, 1938) may or may not have come from trees in the immediate vicinity. As to climate, *Thuja* tells little, for it thrives in the heat of the Shenandoah Valley as well as farther north. Lime seems to be a requisite. *Taxus canadensis*, although more northern in distribution than any other species of *Taxus*, none-the-less now displays too wide a latitudinal range to be interpreted as indicative of a very cold climate. It is thriving under the same climatic conditions as some of the larger-leaved species of *Magnolia* (figs. 4, 5).

The occurrence of prairie plants and prairie communities far to the east of the location of widespread prairie is a well-known phenomenon which needs no discussion here. The Prairie Peninsula extends into central Ohio (see Transeau's map, 1935). Prairie communities are well represented on the Wisconsin drift, where their occurrence is explained by eastward migration during the post-Wisconsin xerothermic period. Whether or not the well developed and often more xeric prairies of unglaciated southern Ohio are of the same age is questionable (Braun, 1928, 1928a). (These are the prairies concerning which Dr. Deevey credits me with the astonishing and incorrect statement that they differ from central Ohio

prairies in that they contain no western species, but instead, coastal plain species!). The problem of age of these prairies is interlocked with that of the occurrence of southern species (both xerophytes and mesophytes) and of pronounced disjuncts (fig. 6) in the same geographic area as the prairies. Information on soil freezing during Pleistocene time, when available, may help to solve these problems.¹ It

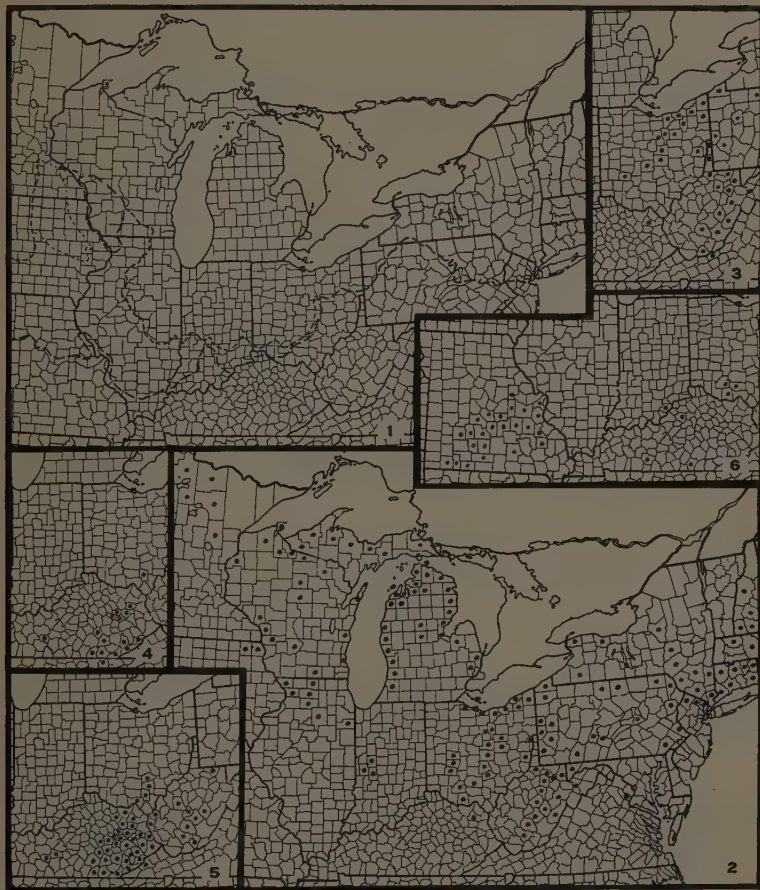


FIGURE 1. Map showing glacial boundary (long dashes) and boundary of Wisconsin glaciation (short dashes) where this is to the north of the limit of glaciation. (Iowan substage shown separate from Des Moines lobe of Wisconsin.)

FIGURES 2-6. Ranges of: (2) *Taxus canadensis* and (3) *Acer spicatum*, northern species with isolated stations south of the glacial boundary; (4) *Magnolia macrophylla*; (5) *Magnolia tripetala*; (6) *Leavenworthia uniflora*, an Ozarkian species with isolated occurrences in prairie communities of unglaciated southern Ohio, southern Indiana, and Kentucky, and in the Cedar Glades of Tennessee.

¹This phenomenon was discussed on the field-trip which followed this symposium. Evidence of congeliturbation, although present, did not indicate severe frost action at a distance of 15 miles from the Wisconsin ice border.

must be remembered that prairie plants today, at latitude 50°N, are subjected to a rigorous climate, perhaps almost as rigorous as that of sheltered spots at latitude 39°N during a glacial age.

The interpretation of the present distribution of southern plants whose ranges overlap, reach, or fall short of the Wisconsin (or other) glacial boundaries is challenging.

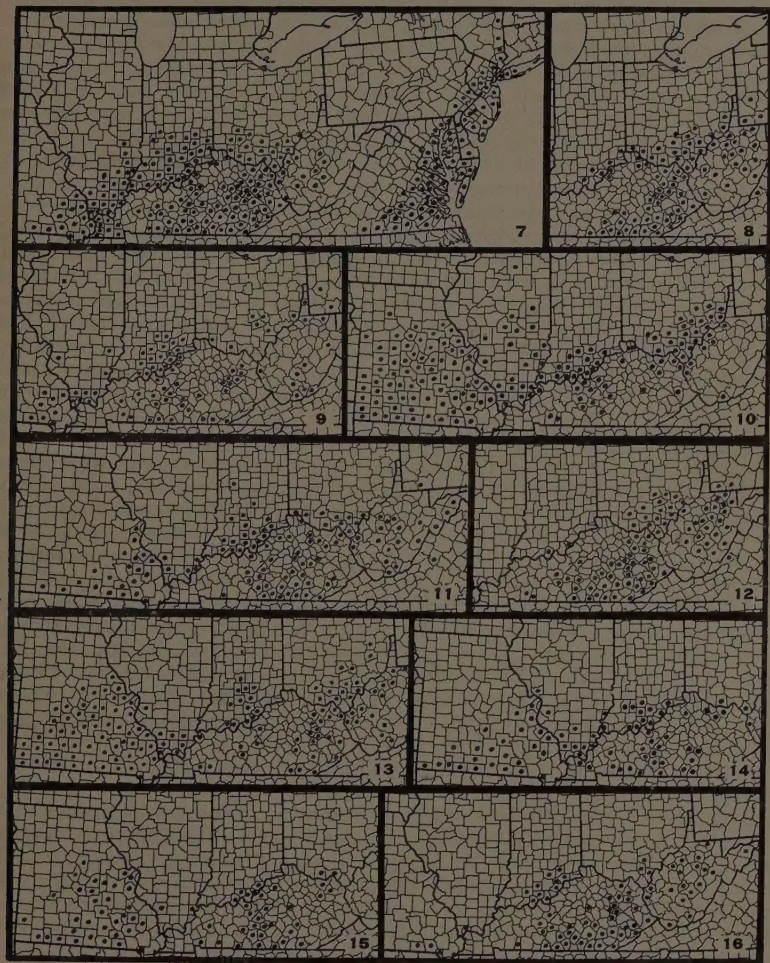
A considerable number of these southern species display evidence (based on behavior in succession) of present or very recent active migration onto the glaciated area. Sweet gum (*Liquidambar*) is one of these (fig. 7). River birch (*Betula nigra*) along most, perhaps all of its sinuous northern boundary is another. However, there are peculiar interruptions in its range in southern Ohio and Indiana (and to a lesser extent, in the range of *Liquidambar*) which correspond with places where the Ohio River was non-existent in pre-Illinoian time, and which need investigation as to possible edaphic or historical cause.

Some species, for example *Aesculus octandra* (fig. 8), have made little progress into glaciated land. This tree is a climax species whose advance must await slow changes of forest environment, and thus far it has been able to move but a short way within the Illinoian drift area, although other climax species, notably beech and sugar maple, have gone far north. A number of shrubby and herbaceous species, at least some of which (for example, *Aralia spinosa*, *Gillenia stipulata*, *Salvia lyrata*) are not climax species or are not dependent on maturity of soil, have comparable distribution patterns (figs. 9, 10, 11). Plants of immature soils or of earlier successional stages should be able to migrate sooner than climax species. For example, redbud (*Cercis canadensis*) has gone far, even though severe winter cold does kill its flower buds. Why not the ones mentioned? And why do the ranges of other such species not extend to the glacial boundary, or at least not to the Wisconsin glacial boundary, although suitable edaphic sites do exist within the glacial boundary?

Many southern plants reach the limits of their more or less continuous geographic ranges a short distance south of the glacial boundary. Others occur in isolated spots south of the glacial boundary but to the north of their area of continuous ranges. Species displaying such distribution patterns have aroused considerable discussion, and as yet there is no decisive evidence as to cause of, or date of origin of such patterns (figs. 4, 5, 12-16). Included here are the large assemblage of species, mostly Appalachian (but which Deevey calls coastal plain), species of which Transeau (1941) and Wolfe (1942) have written. Some of these species are pronounced mesophytes, some are xerophytes. If the present range, or at least its northern part, is of post-Pleistocene date, as Dr. Deevey's thesis asserts, we must account for the northward progress of mesophytes at some date (presumably during a warm moist period) and of xerophytes at some other time (presumably the xerothermic period). But, we must also explain why the ranges of a considerable number of both groups of species—species of very unlike habitats—stop at more or less the same place, and where there are no discernible climatic or soil boundaries. It is this latter feature, and the localization of disjunct occurrences in places unaffected by certain Pleistocene events, that has led to the explanation that ranges were terminated during an ice advance. When we consider the very different microclimates of rugged areas (as Dr. Wolfe has pointed out in this symposium), the existence of small local refugia seems possible, from which repopulation of the surrounding area could have taken place. This brings to mind *Sullivantia*, a plant of moist shaded cliffs near the glacial boundary in Ohio and Indiana, a plant sometimes growing near cave entrances or sinks, where temperatures vary but little.

Certain features of distribution, well marked in the hilly and rugged western border of the Appalachian Plateaus, from southern Ohio southward, are not seen in sections of less relief to the east or to the west. This lends weight to the idea of

Pleistocene refugia in the hilly strip. And if there were such refugia, then a part of the vegetation is old, at least pre-Wisconsin, and if pre-Wisconsin, then just as possibly older.



FIGURES 7-16. Ranges of: (7) *Liquidambar styraciflua*, a southern species actively migrating into glaciated territory; (8) *Aesculus octandra*, (9) *Aralia spinosa*, (10) *Gillenia stipulata*, and (11) *Salvia lyrata*, southern species whose ranges reach or extend slightly into glaciated areas; (12) *Oxydendrum arboreum*, (13) *Cunila origanoides*, (14) *Agave virginica*, (15) *Rhamnus caroliniana*, and (16) *Euonymus americana*, southern species with very unlike edaphic requirements, but whose ranges terminate south of the glacial boundary.

Examination of this rugged western margin of the plateau a little farther south discloses the presence there of at least three local endemics. One, *Conradina verticillata*, is a streambank species; the other two, a *Solidago* and a *Eupatorium*,

are inhabitants of "rock-houses," the most protected sites in the entire area, sites with the least temperature range. They do not grow outside these shelters, a fact which strongly suggests their derivation from milder climate Tertiary species. It also discloses the disjunct occurrence there of a number of species commonly thought of as confined to the Southern Appalachians, and usually referred to as Tertiary relics (*Rhododendron catawbiense*, *Stewartia ovata*, *Astilbe biternata*, for example). Discussion of these under "distribution in relation to the glacial boundary" may seem far-fetched. However, as Deevey's hypothesis states "that glacial chilling in the southeastern States must have been fairly extensive, and that the warmth-loving species, including many or perhaps most of the 'Miocene relicts,' survived in peninsular Florida and in Mexico, and have subsequently migrated to their present localities," it becomes necessary to consider these Tertiary relics in connection with glacial border phenomena. There is no evidence to support the hypothesis that the "Miocene relicts" lived in Florida during the Pleistocene. In Florida peat deposits, pollens of pines, oaks, hickories, grasses, ferns, palms, etc., are found along with spruce and fir pollen (Davis, 1946), but pollens of mesophytes and Appalachian species are absent. Neither is there evidence of Mexican abode. Just because a number of widespread eastern American plants—"typical plants of the eastern United States," to use Fernald's words (1950)—have been found in the mountains of Mexico, it cannot be assumed that the rare and local "Miocene relicts" migrated there and, returning, became concentrated in or about the Southern Appalachians. Moreover, the idea of making peninsular Florida a veritable Noah's ark for plants does not take into consideration the edaphic requirements of the plants concerned. Can anyone who has seen *Diphyllaea*, for instance, in the cool, moist coves of the Smokies, imagine it in a coastal plain environment? Deevey apparently contradicts himself in this respect, for while discussing the Pine Barrens he says that it is "doubtful that the Pine Barrens or any other part of the coastal plain constituted an *important* refuge for mesophytic species." However, when he wants to dispose of the "Miocene relicts" of the Southern Appalachians, he postulates that they must have gone to the Floridian section of the Coastal Plain, or, crossing a great extent of plains, to the mountains of Mexico. He inconsistently assumes that the Southern Appalachian endemics could not have stayed in this geographic area, while beech stayed in the northern Appalachians, and hickory in the Middle West. (He speaks of "beech, moving out from its center of refuge in the northern Appalachians" and of "hickory, moving eastward from centers of refuge in the middle West."). But why dispose of the Tertiary relics? Because "Cooling sufficient to permit the growth of spruce and fir forests on the summits of the Appalachians should have wiped out the remarkable relicts of the Miocene flora, some of which now occur on some of the same summits." This statement seems to imply post-Pleistocene re-entry of these "relicts of the Miocene flora." However, as spruce and fir forests *now* occupy the summits and upper slopes of some of the Southern Appalachians, and the Tertiary relics are there, too, it is reasonable to believe that such a combination of species could have been present in glacial ages, as now, and could have persisted since Tertiary time.² All of the evidence indicates that they are localized in and around the Southern Appalachians because this area was, in middle Tertiary time, the only large mountainous area of the East, and that they have continued to occupy this area to the present time (Braun, 1950, Chapters 16, 17).

A significant feature, and the one which best justifies discussion of Southern Appalachian plants in this paper is that recent investigations (King and Stupka, 1950) have shown that there was a timber-line in the Great Smoky Mountains—probably in the last cold phase of the Pleistocene; and that this timber-line was at

²The fir (*Abies Fraseri*) is a Southern Appalachian endemic, *not* a northern species; the spruce (*Picea rubens*) is not a constituent of the boreal forest.

an elevation between 4000 and 5000 feet (more than that above the lowered ocean of glacial stages). The higher peaks now extend above the spruce and the spruce-fir zones, and are occupied by Fraser fir forests; they are close to a tree limit. Depression of altitudinal belts by 2000 feet, the amount indicated by recent studies, would still allow a band 1000 to 2000 feet in vertical height to serve as a refuge for plants forced to move to lower and warmer belts, belts below the spruce zone in which a number of the endemics occur. This lower band, up to an elevation of 3000 feet, more or less, and all the surrounding area in all directions, would have been suitable for the growth of deciduous forest—as it is today. The Wisconsin glacial border was less than 250 miles to the north of the Great Smoky Mountains, and if zones were depressed as rapidly as 1000 feet for every hundred miles, this would bring the deciduous forest zone to the plateau level about 50 miles south of the ice. Or, depression might have been gradual at first, more rapid as the ice margin was approached. Very few spots in the northern half of the rugged western border of the Cumberland and Allegheny Plateau reach an elevation as high as 1400 feet. A band, 50 miles wide, to the south of the southern lobe of the ice sheet in Ohio, would seem to be more than adequate, as topography in the vicinity of Morgantown, W. Va., does not appear to indicate periglacial conditions (Denny, this symposium). Morgantown is little farther from the glacial border (which is to the west as well as to the north) than is the southern tip of Ohio, and about 75 miles farther north. Furthermore, as the evidence, to date, does not “furnish unequivocal proof of the presence of permafrost” even in northern Pennsylvania, 200 miles north of and over 1000 feet higher than the Ohio and Kentucky areas where species distribution indicates Pleistocene survival, there appears to be no sound reason for postulating complete southward retreat of deciduous forest species.

We may believe, then, that the deciduous forest zone, although narrowed, maintained itself on the Appalachian Plateaus in southern Ohio and Kentucky while glaciers extended southward in Ohio. Most of its species can endure temperature extremes far greater than those in this area today. We may believe, then, that during glacial epochs, some species now showing a spotty distribution near the glacial boundary may have persisted in local favorable habitats. We may believe, also, that the ranges of many southern and Appalachian species were abruptly terminated at varying distances south of the glacial boundary. These have been able to advance greater or less distances toward or onto the glaciated area.

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(Some additional data from the author's records and from manuscript maps prepared a number of years ago by E. N. Transeau. Additional data from West Virginia supplied by Nelle Ammons; for Illinois, by G. N. Jones; for Missouri, by J. A. Steyermark.)

ANIMALS OF THE GLACIAL BORDER¹

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SUMMARY

The glacial border has a rich and diversified fauna in correlation with the wide range of habitats fringing the glacial boundary. The large complex of species has had diverse sources of origin and represents migrations during a number of periods from the Tertiary to the present.

The various elements listed are as follows: (1) Allegheny Plateau fauna, (2) northern relicts, (3) immigrants from the Atlantic seaboard in early post-glacial time, (4) immigrants from the south and southwest of the glacial boundary, (5) invaders from the west during the Xerothermic Period, and (6) species which have extended their ranges as a result of occupation of the land by Europeans.

The distribution of certain species seems to indicate that they may have persisted not far from the ice front throughout Wisconsin time, perhaps throughout the Pleistocene.

¹This paper, in modified and expanded form, will be published later in THE OHIO JOURNAL OF SCIENCE as the presidential address before the Ohio Academy of Science.